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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

HAROLD ST. JOHN

Revision of the Genus Pandanus
Part 14. Malaya and Singapore

GEORGE W. BARLOW

Species Structure of Gillichthys mirabilis

TAKASHI OKUTANI

Molluscan Assemblages of Izu Submarine Banks

WILLIAM A. GOSLINE

Osteology and Systematics of Elongate Perciform Fishes

LINDSAY R. WINKLER and E. YALE DAWSON

Food Habits of California Sea Hares

D. L. INMAN, W. R. GAYMAN, and D. C. COX

Littoral Sedimentary Processes on Kauai

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(Continued on inside back cover)

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MAR 25 1963

Revision of the Genus *Pandanus* Stickman, Part 14 New Species from Malaya and Singapore

HAROLD ST. JOHN¹

AS A RESULT of field work in Malaya and Singapore and of study in the herbarium at Singapore, numerous new species of *Pandanus* have been detected. The following novelties are of this origin.

Pandanus attenuatus sp. nov. (sect. *Acrostigma*)

Fig. 150

DIAGNOSIS HOLOTYPI: Frutex probabaliter humili, caule in apice 8 mm diametro lutescenti laevi sed cum dorsis longitudinalibus, foliis 35–40 cm longis 18–20.5 mm latis chartaceis supra viridibus infra minime viridibus pallidioribus et proxima basem purpureo-tinctis 1-costatis et minime 2-plicatis subplanis in sectione mediali cum 14–15 nervis parallelis secundariis prominentibus in quoque dimidio nervis tertialis subvisibilis infra proxima apicem, lamina ligulata subito in apice caudato 5.5–6 cm longo 0.7 mm lato contracto basi amplexicauli inermi valde nervosa sed ex 2 cm marginibus cum aculeis 0.5–1.3 mm longis 2–6 mm distantibus subulatis adscendentibus pallidis, midnervo infra ultra mediam inermi, in sectione mediali marginibus cum aculeis 0.7–1 mm longis 1–4 mm distantibus subulatis valde adscendentibus, apice subulato cum marginibus et midnervo infra cum aculeis 0.5–1 mm longis 0.5–1 mm separatis subulatis adscendentibus, inflorescentia foeminea terminali adscendenti cum 1 syncarpio, pedunculo 4.5 cm longo 4 mm diametro trigono bracteato, syncarpio 3.5 cm longo 2.7 cm diametro ellipsoideo cum circa 144 drupis eis 13–13.5 mm longis 4–4.5 mm latis crassisque fusiformibus 5–6-angulosis corpore 6–7 mm longo, pileo 7.5–9 mm longo basi 3.5–4 mm alto ovoideo subanguloso laevi, stylo 4–6 mm longo valde proxime arcuato osseoso subulato olim in basi subanguloso, stigmatibus 4–4.5 mm longo late lineari brunneo papilloso in apice extento, endo-

carpio in parte $\frac{1}{3}$ infera lateribus cartilagineis pallidis, seminibus 3.5–4.5 mm longis subdoliiformatis, mesocarpio apicali hemisphaerico, mesocarpio basali sparso cum fibris fortibus in lateribus.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Shrub, probably low; stem at apex 7–8 mm in diameter, yellowish, smooth but with longitudinal ridges; leaves 35–40 cm long, 18–20.5 mm wide, chartaceous, green above, below slightly paler green and near the base suffused with purple, 1-ribbed, slightly 2-pleated, but nearly flat, at midsection with 14–15 parallel secondary veins in each half, these prominent throughout, cross tertiary veins barely visible only below and near the tip, the blade ligulate, abruptly contracted to a 5.5–7.5 cm caudate tip, this 0.7 mm wide, the base amplexicaul, unarmed, very veiny, beginning 2 cm up the margins with prickles 0.5–1.3 mm long, 2–6 mm apart, subulate, ascending, pale; the midrib below unarmed to beyond the middle; at midsection the margins with prickles 0.7–1 mm long, 1–4 mm apart, subulate, sharply ascending; the subulate apex having the margins and midrib below with prickles 0.5–1 mm long, 0.5–1 mm apart, subulate, ascending; pistillate inflorescence terminal, ascending, bearing 1 syncarp; peduncle 3.5–4.5 cm long, 4 mm in diameter, 3-sided, bracted; syncarp 3–3.5 cm long, 2.7 cm in diameter, ellipsoid, bearing about 120–144 drupes, these 13–13.5 mm long, 4–4.5 mm thick and wide, fusiform, 5–6-angled, the body 6–7 mm long; pileus 7.5–9 mm long, the base 3.5–4 mm high, ovoid, slightly angled, smooth; style 4–6 mm long, sharply curved proximally, bony, subulate, slightly angled only on the base; stigma 4–4.5 mm long, broad linear, brown, papillose, running to the tip; endocarp centering in lower $\frac{1}{3}$, but extending to the base, the walls cartilaginous, pale; seed 3.5–4.5 mm long, more or less barrel-shaped; apical mesocarp hemispheric, with the center hollow; basal mesocarp sparse, with strong fibers up the sides.

¹ B. P. Bishop Museum, Honolulu 17, Hawaii, U. S. A. Manuscript received June 29, 1961.

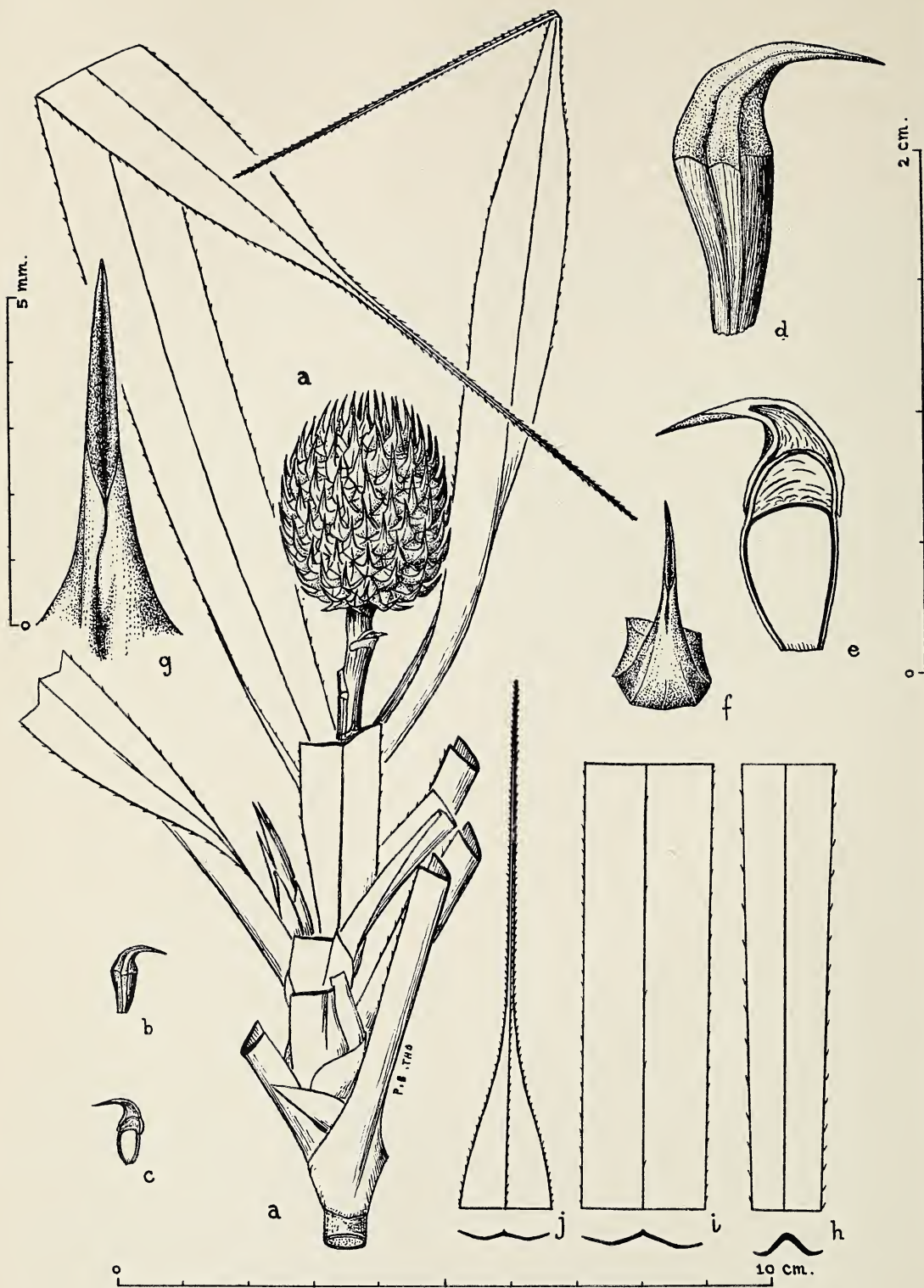


FIG. 150. *Pandanus attenuatus* St. John, from holotype. *a*, Habit, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, apical view, $\times 4$; *g*, style and stigma, oblique view, $\times 10$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$.

HOLOTYPE: Malaya, Selangor, Gunong Ielu Semangkok, 28 April 1922, I. H. Burkill 8,876 (SING).

SPECIMENS EXAMINED: Malaya, Selangor, Gap Sempadang, 1908, Hashin (SING).

DISCUSSION: *P. attenuatus* is a member of the section *Acrostigma*, as is its closest relative, the Malayan *P. unguiculatus* Ridl., which has the leaves 21–27 mm wide, at midsection with 17–19 secondary veins in each half; syncarp 5.5 cm long; drupes 18–20 mm long; the seed 7–8 mm long, suprabasal; and the style 2.5–3 mm long. *P. attenuatus* has the leaves 18–20.5 mm wide, at midsection with 14–15 secondary veins in each half; syncarp 3–3.5 cm long; drupes 13–13.5 mm long; seed 3.5–4.5 mm long, basal; and the style 4–6 mm long.

The new epithet is the Latin word *attenuatus*, drawn out, which is given in allusion to the attenuate subulate leaf apex.

Pandanus caudatifolius, nom. nov. (sect. *Acrostigma*)
Fig. 151

P. globuliferus Ridl., R. Asiat. Soc., Straits Br., Jour. 61: 42, 1912; non Thouars (1808).

DIAGNOSIS OF HOLOTYPE: "Stems up to 1 m tall," 6–7 mm in diameter, yellowish, smooth; leaves 33–37 cm long, at the middle 15–17 mm wide, near the base 10–11 mm wide, firm chartaceous, dark green above, pale below, almost flat except at base, swordlike, tapering in lower 1/3 to the narrower base, in upper 1/3 rather sharply narrowed to the 7 cm subulate apex, this 5 cm down 1 mm wide, the secondary parallel veins conspicuous and at midsection 15 in each half, no visible tertiary cross veins, the base widened and amplexicaul, unarmed, but beginning at 2–2.5 cm the margins with prickles 0.8–1 mm long, 2–4 mm apart, subulate, straight or arcuate, ascending, pale; the midrib below unarmed for lower 3/4; at midsection the margins with subulate tipped serrae 0.2–0.3 mm long, 1.5–3 mm apart; on the caudate triangular apex the margins and midrib below with prickles 0.5–0.9 mm long, 1–3.5 mm apart, stout subulate, arcuate, ascending; peduncle 3 cm long; syncarp 18 mm in diameter, globose, bearing about 40 drupes, these 11–13 mm long, 3.5–4 mm wide,

2–3 mm thick, the body oblanceoloid, compressed, narrowed to the subulate style, 5–6 angled, the body 8–9 mm long; pileus 6–7 mm long, its base the widest part of the drupe, the lower part pyramidal-semiorbicular; style 3–4 mm long, subulate, ascending arcuate; stigma distal, 2.5–3 mm long, linear, extending to apex, brown, papillose; endocarp in lower 1/4, obconic, the base obtuse, stramineous, dull, cartilaginous, the walls 0.2 mm wide; apical mesocarp 3.5–4 mm long, a cavern filled with white medullary membranes and hairs; basal mesocarp sparse, the margins fibrous, the center fleshy.

HOLOTYPE: Malaya, Selangor, Gunong Semangkok, 4,000 ft. alt., April 1894, H. N. Ridley 15,612 (SING).

DISCUSSION: *P. caudatifolius* is a member of the section *Acrostigma*, as is its closest relative, *P. globosus* St. John, a Malayan species with the leaves 11–12 mm wide, little if at all narrowed towards the base, at midsection the margins with prickles 1–1.5 mm long, 2–5 mm apart, subulate; drupes 14–17 mm long; and the style 3–6 mm long. *P. caudatifolius* has the leaves 15–17 mm wide near the middle, ligulate, narrowed below and near the base 10–11 mm wide, at midsection the margins with subulate-tipped serrae 0.2–0.3 mm long, 1.5–3 mm apart; drupes 11–13 mm long; and the style 3–4 mm long.

The epithet is derived from *caudatus*, having a tail, and *folium*, leaf, given in reference to the appearance of the leaf.

Pandanus globulosus sp. nov. (sect. *Acrostigma*)
Fig. 152

DIAGNOSIS HOLOTYPE: Frutex, caulibus in apice 6–7 mm diametro laevibus lucidis lutescentibus, foliis 38–42 cm longis 11–12 mm latis firme chartaceis supra obscure viridibus infra pallide viridibus et ad basem purpureis 1-costatis licet paene planis, in sectione mediali cum 12–14 nervis parallelis secundariis in quoque dimidio eis ubique prominentis, nervis tertialis nullis, laminis ligularis subabrupte contractis in apice caudato subulato 5.5–6.5 cm longo 0.5 mm lato basi amplexicauli inermi conspicue nervosa ex 2–3 cm marginibus cum aculeis 0.5–0.9 mm longis 2.5–7 mm distantibus subulatis proxime adscendentibus pallidis, midnervo per 30 cm in-

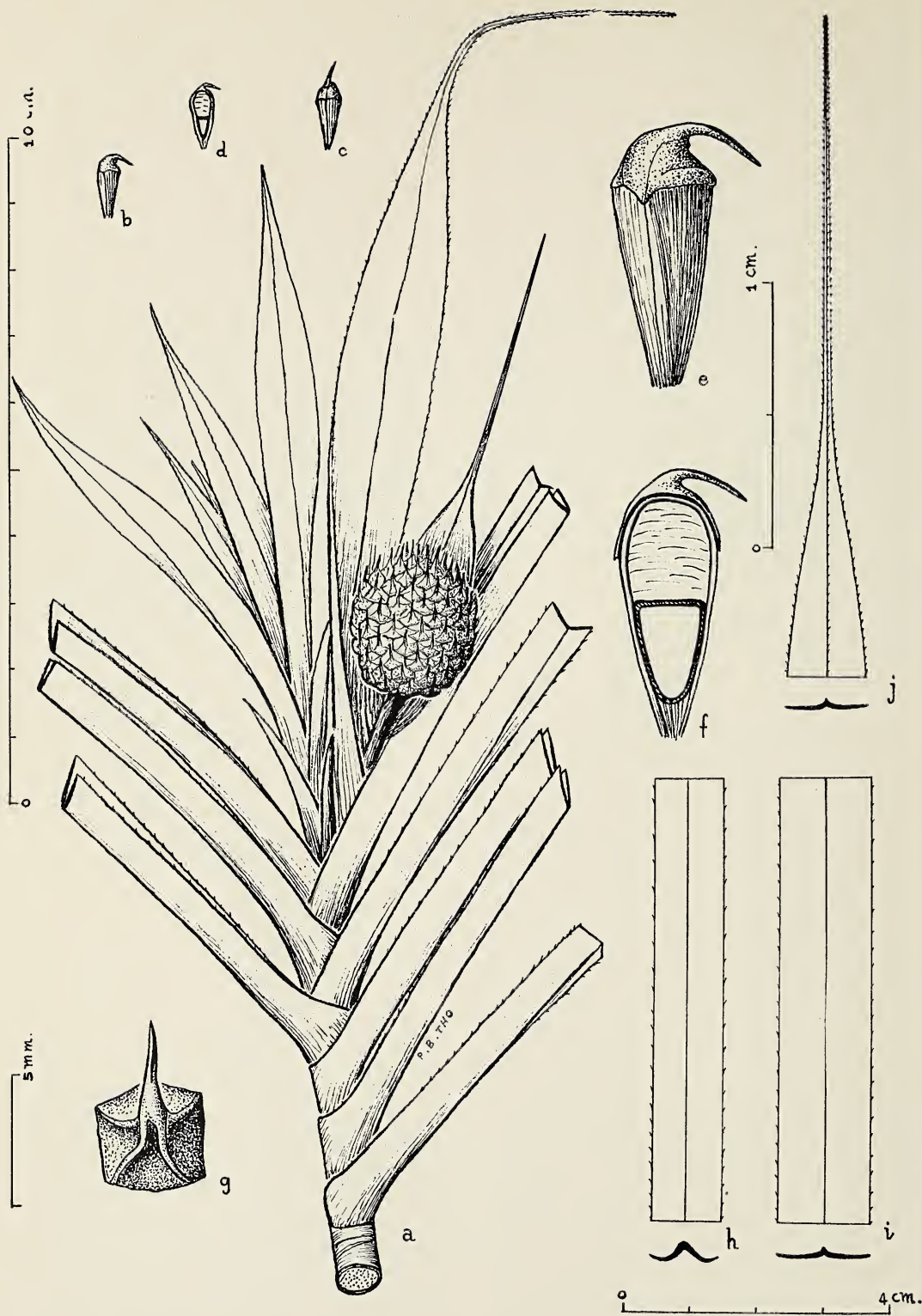


FIG. 151. *Pandanus caudatifolius* St. John, from holotype. *a*, Habit, $\times 1$; *b*, *c*, drupes, lateral view, $\times 1$; *d*, drupe, longitudinal median section, $\times 1$; *e*, drupe, lateral view, $\times 4$; *f*, drupe, longitudinal median section, $\times 4$; *g*, drupe, apical view, $\times 4$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$.

ermi, in sectione mediali marginibus cum aculeis 1–1.5 mm longis 2–5 mm distantibus proxime adscendentibus subulatis, in apice caudato marginibus et midnervo infra cum aculeis 0.7–1 mm longis 0.7–3.5 mm distantibus subulatis adscendentibus, inflorescentia foeminea terminali erecta cum uno syncarpio, pedunculo 4–6 cm longo 3–4 mm diametro trigono bracteato, syncarpio 2.5–3.5 cm longo 2.3–3 cm diametro globoso vel elliptici-globoso cum circa 96–120 drupis eis 14–17 mm longis 3–4.5 mm latis crassisque fusiformibus sed apice angustiori 5–6-anguloso, corpore 9–10 mm longo oblanceoloido, pileo 7–11 mm longo basi 3–5 mm alta ovoidea vel oblato-ovoidea cum 5 angulis prominentibus laevibus, stylo 3–6 mm longo proxime arcuato subulato rigido, stigmatibus 2–3 mm longo lineari distali brunneo papilloso in apice extento, endocarpio in parte $\frac{1}{3}$ infera obconico lateribus 0.2 mm crassis cartilagineis stramineis, mesocarpio apicali suborbiculari cum membranis albis radiatis numerosis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Shrub; stems at summit 6–7 mm in diameter, smooth, shining, yellowish; leaves 38–42 cm long, 11–12 mm wide, firm chartaceous, dark green above, pale green below and with a small area near the base purple, 1-ribbed, apparently almost flat, at midsection with 12–14 parallel secondary veins in each half, these prominent throughout, no visible tertiary cross veins, the blade ligulate, rather abruptly contracted to a 5.5–6.5 cm subulate, caudate apex, this 0.5 mm wide, the base amplexicaul and unarmed, prominently veiny, beginning at 2–3 cm up the margins with prickles 0.5–0.9 mm long, 2.5–7 mm apart, subulate, closely ascending, pale; midrib unarmed for about 30 cm; at midsection the margins with prickles 1–1.5 mm long, 2–5 mm apart, closely ascending, subulate; on the caudate apex the margins and midrib below with prickles 0.7–1 mm long, 0.7–3.5 mm apart, subulate, ascending; pistillate inflorescence terminal, erect, bearing 1 syncarp; peduncle 4–6 cm long, 3–4 mm in diameter, 3-sided, bracteate; syncarp 2.5–3.5 cm long, 2.3–3 cm in diameter, globose or elliptic-subglobose, bearing about 96–120 drupes, these 14–17 mm long, 3–4.5 mm wide and thick, fusiform but the tip more slender,

5–6-angled, the body 9–10 mm long, oblanceoloid; pileus 7–11 mm long, the base 3–5 mm high, ovoid or oblate-ovoid, with 5 prominent angles, smooth; style 3–6 mm long, curved proximally, subulate, rigid; stigma 2–3 mm long, linear, distal, brown, papillose, running to the tip; endocarp in lower $\frac{1}{3}$, obconic, the walls 0.2 mm thick, cartilaginous, stramineous; apical mesocarp suborbicular, with numerous radial, white membranes; basal mesocarp sparse, fibrous and fleshy.

HOLOTYPE: Malaya, Pahang, Telom ridge, Nov. 1908, *H. N. Ridley* 13,798 (SING).

DISCUSSION: *P. globulosus* is a member of the section *Acrostigma*, as is its closest relative, the Malayan species *P. caudatifolius* St. John. Under that species is given a summary of the contrasting differences.

The epithet is the Latin adjective *globulosus*, like a little sphere, and is chosen with reference to the shape of the syncarp.

Pandanus mollifoliaceus sp. nov. (sect. *Acrostigma*)

Fig. 153

DIAGNOSIS HOLOTYPI: Frutex, caule in apice 8 mm diametro luteo laevi, foliis 45–47 cm longis 23–29 mm latis molliter chartaceis supra viridibus infra pallide viridibus et videtur glaucis 1-sulcatis 2-plicatis in sectione mediali cum 17–18 nervis secundariis parallelis in quoque dimidio eis ubique prominentibus, circa apicem infra nervis tertialis reticulum cum sectionibus oblongis formantibus, lamina ligulata circa mediam latissima proxima basem 14–15 mm latis, in 6.5 cm apice caudato subiter diminuentibus eo 5 cm ex apice 0.7 mm lato, basi amplexicauli inermi et nervis exevidentibus, marginibus ex 3 cm cum aculeis 1–1.5 mm longis 2–5 mm distantibus subulatis pallidis in 45° adscendentibus, midnervo per 35 cm inermi, in sectione mediali marginibus cum aculeis 0.5–1 mm longis 4–10 mm distantibus subulatis adpresse adscendentibus, in apice contractenti marginibus cum aculeis 0.8–1.7 mm longis 2.5–3.5 mm distantibus divergentibus, midnervo infra cum aculeis simulantibus 4–7 mm distantibus, in apice caudato marginibus et midnervo infra cum subulato-serrulis 0.5–0.9 mm longis 2–4 mm distantibus, inflorescentia foeminea terminali erecta cum uno

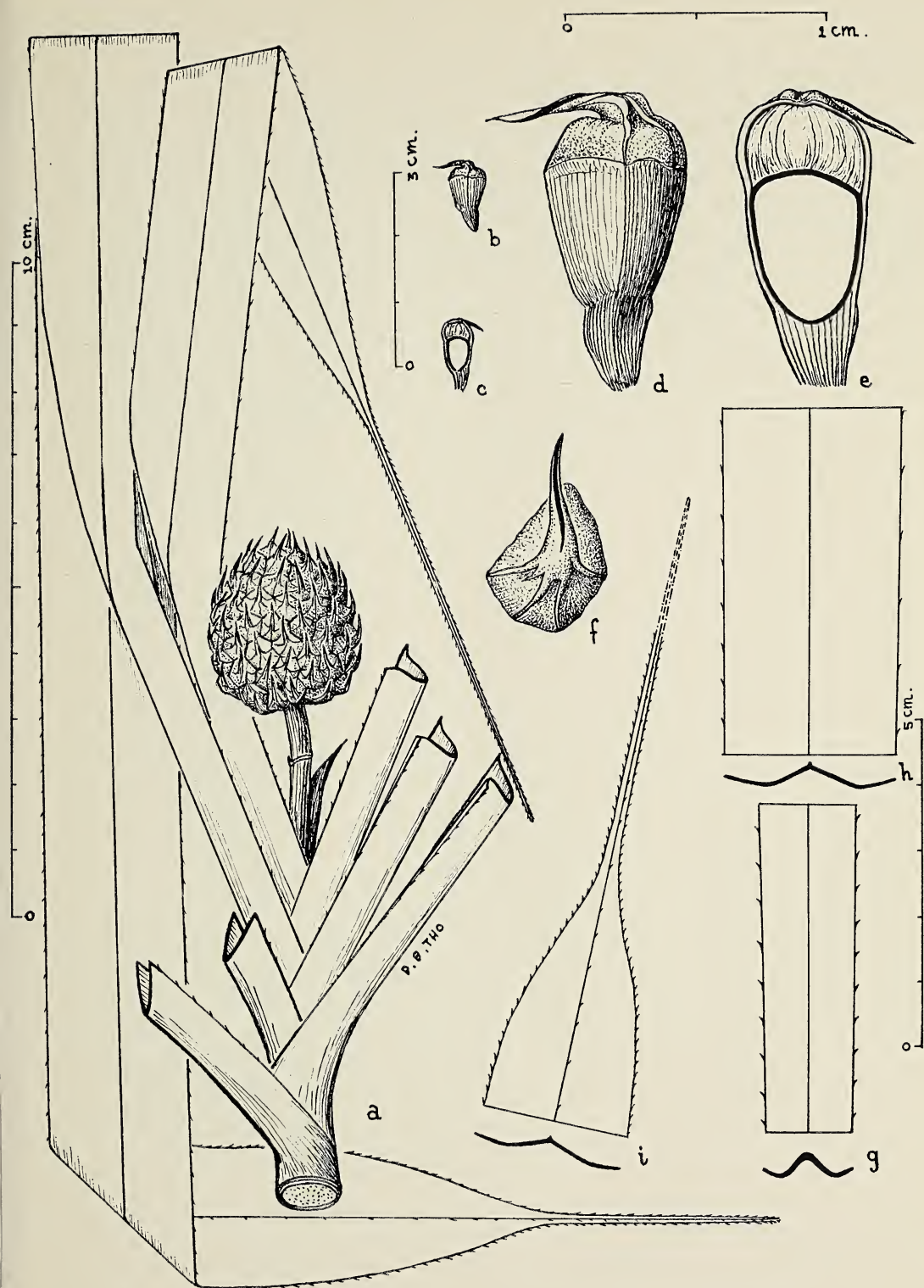


FIG. 153. *Pandanus mollifoliaceus* St. John, from holotype. *a*, Habit, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, style, and stigma, apical view, $\times 4$; *g*, leaf base, lower side, $\times 1$; *h*, leaf middle, lower side, $\times 1$; *i*, leaf apex, lower side, $\times 1$.

capite, pedunculo 3 cm longo 3 mm diametro trigono bracteoso, syncarpio 2.7 cm longo 2.3 cm diametro subgloboso cum circa 120 drupis eis 8–10 mm longis (vel in curvatura styli sequi 12–15 mm) 4–5 mm latis 3–4 mm crassis corpore oblongo-ovoideo 5-anguloso lateribus striatis, pileo cum basi 2 mm alta pulviniformi 5-angulato minute striato, stylo 4–5 mm longo proxime in angulo recto curvato recto vel sinuoso subulato gracile firmo in dimidia infera anguloso, stigmatate 3–4 mm longo lineari distali brunneo paene in apice extento, endocarpio in tertia infera 5–6 mm longo late obovoideo lateribus 0.2 mm crassis cum fibris longitudinalibus fortibus et membrano gracili pallidi, mesocarpio apicali cavernoso cum membranis medullosis albis paucis, mesocarpio basali carnosio et cum fibris tenuibus.

DIAGNOSIS OF HOLOTYPE: Shrub; stem 8 mm in diameter at apex, yellowish, smooth; leaves 45–47 cm long, 23–29 mm wide, soft chartaceous, green above, pale green and apparently glaucous below, 1-ribbed, 2-pleated, at midsection with 17–18 parallel secondary veins in each side, these prominent throughout, and on the lower side near the tip with barely visible cross tertiary veins making irregular oblong meshes, the blade ligulate, though broadest at or beyond the middle, near the base 14–15 mm wide, abruptly contracted to a 6.5 cm caudate tip, this 5 cm down 0.7 mm wide, the base amplexicaul, unarmed, the veins obscure, beginning 3 cm up the margins with prickles 1–1.5 mm long, 2–5 mm apart, subulate, pale ascending at about 45°; the midrib unarmed for about 35 cm; at midsection the margins with prickles 0.5–1 mm long, 4–10 mm apart, subulate, closely ascending; on the subapical contracting region the margins with prickles 0.8–1.7 mm long, 1.5–2.5 mm apart, divergent, and those of the midrib below similar but 4–7 mm apart; on the caudate tip the margins and midrib below with subulate serrulations 0.5–0.9 mm long, 2–4 mm apart; pistillate inflorescence terminal, erect, bearing one head; peduncle 3 cm long, 3 mm in diameter, 3-sided, bracteate; syncarp 2.7 cm long, 2.3 cm in diameter, subglobose, bearing about 120 drupes, these 8–10 mm long (or following the curve of the style 12–15 mm), 4–5 mm wide, 3–4 mm thick, the body oblong-obovoid,

5-angled, the sides striate; pileus with the base 2 mm high, cushion-shaped, 5-angled, finely striate; style 4–5 mm long, proximally ascending at right angles, straight or twisting, slender subulate, firm, angled in lower half; stigma 3–4 mm long, linear, distal, brown, running almost to the tip; endocarp centering in lower $\frac{1}{3}$, and 5–6 mm long, broadly obovoid, the walls 0.2 mm thick, of heavy longitudinal fibers and a thin connecting membrane, pale; apical mesocarp a broad cavern with a few white medullary membranes; basal mesocarp fleshy and with weak fibers.

HOLOTYPE: Malaya, Negri Sembilan, Gunung Angsi, eastward on ridge, 2,600 ft. alt., 24 Nov. 1923, *Mohamed Nur 11,691* (SING).

DISCUSSION: *P. mollifoliaceus* is a member of the section *Acrostigma*, as is its closest relative, *P. caudatifolius* St. John, of Malaya, a species with its leaves 15–17 mm wide, firm chartaceous, tapering from the middle downwards and near the base only 10–11 mm wide, at midsection the leaf margins with subulate tipped serrae 0.2–0.3 mm long, 1.5–3 mm apart; syncarp 18 mm in diameter, globose, bearing about 40 drupes; drupes with the body oblanceoloid, the sides smooth; pileus base pyramidal-semiorbicular; stigma 2.5–3 mm long; endocarp in lower $\frac{1}{4}$, obconic; and the apical mesocarp longer than wide. *P. mollifoliaceus* has its leaves 23–29 mm wide, soft chartaceous, tapering downwards and near the base 14–15 mm wide, at midsection the leaf margins with prickles 0.5–1 mm long, 4–10 mm apart, subulate; syncarp 2.7 cm long, 2.3 cm in diameter, subglobose, bearing about 120 drupes; drupes with the body oblong-obovoid, the sides striate; pileus base cushion-shaped; stigma 3–4 mm long; endocarp in lower $\frac{1}{3}$, broadly obovoid; and the apical mesocarp wider than long.

The new epithet is formed from the Latin *mollis*, soft; *foliaceus*, leafy, in reference to the soft texture of the leaves.

Pandanus albibracteatus sp. nov. (sect. *Pandanus*)

Figs. 154, 155, 169, 170a

DIAGNOSIS HOLOTYPI: Arboriformis, caulibus 8 m altis 15 cm diametro viridarium formans, cortice brunneo muricato, radicibus fulturosis 1

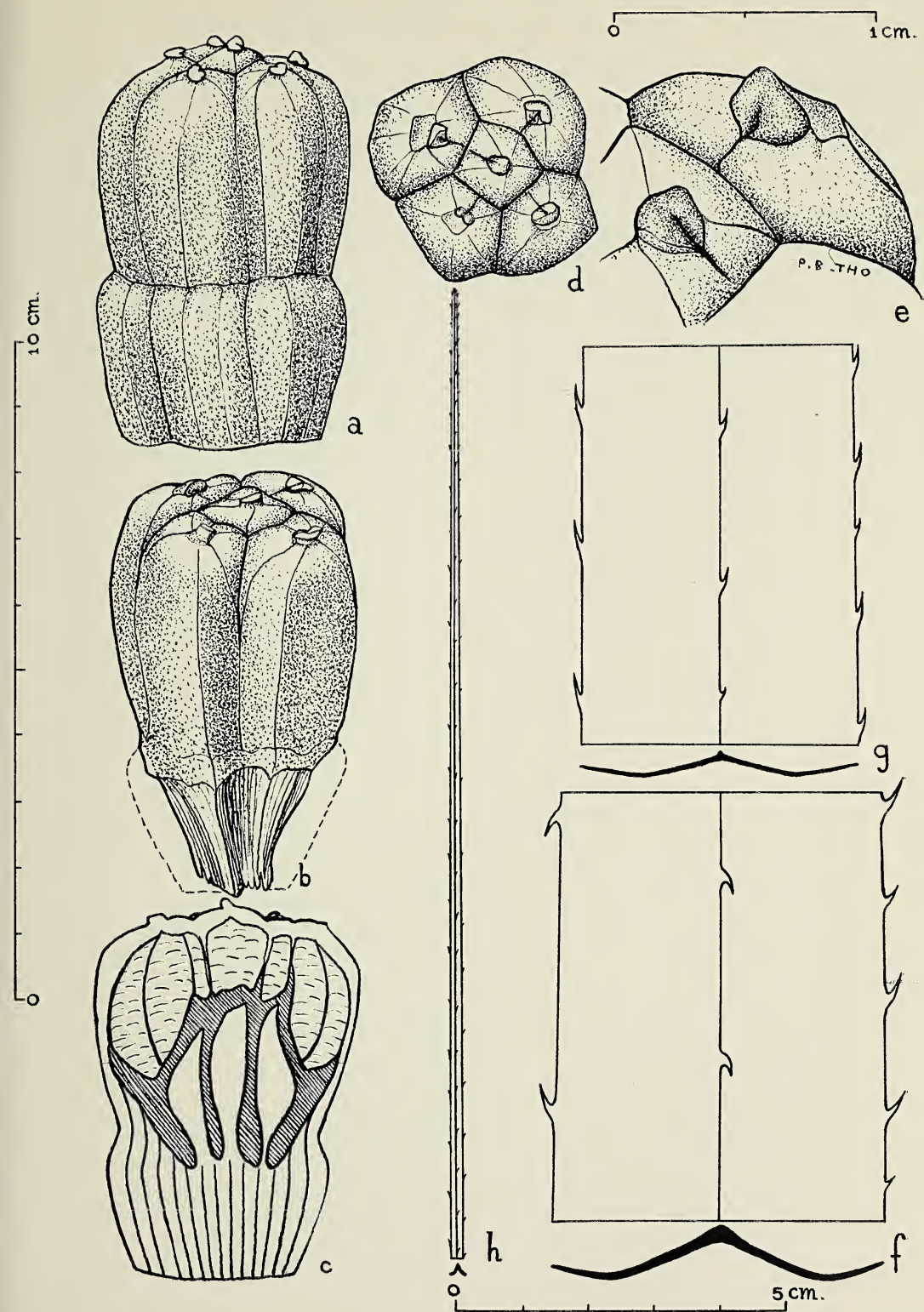


FIG. 154. *Pandanus albibracteatus* St. John, from holotype. *a*, Fresh drupe, lateral view, $\times 1$; *b*, dried drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, apical view, $\times 1$; *e*, carpel apices, stigmas, and proximal sinuses, oblique view, $\times 4$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$; *h*, leaf apex, lower side, $\times 1$.

m longis 3–4 cm diametro in lineis muricatis, foliis 1.72–1.97 m longis 5–5.5 cm latis coriaceis olivaceo-viridibus supra glaucis infra glaucioribus supra midnervum sulcatis 2-plicatis in sectione mediali cum 41–44 nervis parallelis secundariis in quoque medio nervis tertialis nullis infero folii ligulato medio exteriori gladi-formati sensim in apice 40 cm longo caudato subulato trigono diminuenti eo 10 cm ex apice 0.9 mm lato, basi amplexicauli et inermi sed ex 2–6 cm marginibus cum aculeis 4.5–7 mm longis 10–45 mm separatis subulatis rectis vel arcuatis apicibus rubro-brunneis plerumque adscendentibus, midnervo infra cum aculeis 3.5 mm longis 20–45 mm separatis conico-subulatis reflexis, in sectione mediali marginibus cum aculeis 3–5 mm longis 7–20 mm separatis subulatis adpresse adscendentibus, midnervo infra cum aculeis 3.5–4 mm longis 22–28 mm separatis crassiter subulatis adscendentibus, in apice subulato marginibus et midnervo infra cum subulato-serrulis 0.3–0.5 mm longis 4–10 mm separatis; inflorescentia foeminea terminali arcuata cum syncarpio solitario, pedunculo 27 cm longo 13–20 mm diametro trigono folioso-bracteato, syncarpio 23 cm longo 17.5 cm diametro ellipsoideo-subglobose cum 67 phalangibus, nucleo maturo molli et carnosio subito contracto in reliquum minutum, phalangibus 5.5–6.2 cm longis dimidio supero 3.2–4 cm lato 2.5–3.5 cm crasso oblongo-ellipsoideo vel obovoideo infra aurantiaco-rubro supra subviridibus, deinde rosaceo 5–6-anguloso lateribus laevibus sublucidis subconvexis, suturis lateralibus plerumque nullis rariter 1 (–2), apice convexo, sinibus apicalibus centralibus 0.7–2 mm profundis V-formatis in fondam plerumque rectis, dimidio infero phalangiis 3.3–4.2 cm latis 2.8–3.9 cm crassis carnosio-incrassatis rosaceo-aurantiacis cuneato-oblongis humeris 3–6 mm latis 5–8-angulosis lateribus gradatim curvatis carne saccharosa innoxia sed non consumpta, carpellis 4–7 eis centralibus $\frac{2}{3}$ tam grandibus quam marginalibus, apicibus depresso-conico eis marginalibus asymmetricis et aliquis cum plano vel concavo distalo stigmatibus, stigmatibus 2.5–4 mm longis cordatis vel deltoideis vel reniformibus pallide brunneis papillosis sulcatis obliquis centripetalibus, sinibus proximalibus $\frac{1}{2}$ – $\frac{2}{3}$ ad fondam extentis, endocarpio minime supra-mediali osseoso mahogani-colorato intra lucido

lateribus 5 mm crassis, seminibus 12–15 mm longis 5 mm diametro ellipsoideis, mesocarpio supero in quoque apice cavernam cum fibris paucis et membranarum albis medullosis multis formantibus, mesocarpio basali grande fibroso et carnosio.

DIAGNOSIS OF HOLOTYPE: Treelike; stems 8 m tall, 15 cm in diameter, forming a large clump; bark brown, muricate; prop roots 1 m long, 3–4 cm in diameter, muricate in lines; leaves 1.72–1.97 m long, 5–5.5 cm wide, coriaceous, olive green, above glaucous and more so below, broad furrowed above the midrib, and with 2 rounded pleats, at midsection with 41–44 secondary parallel veins in each half, no tertiary cross veins, lower half ligulate, outer half sword-shaped, gradually tapering to a 40 cm caudate subulate trigonous apex, this 10 cm down only 0.9 mm wide, the base amplexicaul and unarmed, but beginning at 2–6 cm the margins with prickles 4.5–7 mm long, 10–45 mm apart, subulate, mostly ascending, straight or arcuate, red-brown-tipped; the midrib below with prickles 3–5 mm long, 20–45 mm apart, conic-subulate, reflexed; at midsection the margins with prickles 3–5 mm long, 7–20 mm apart, subulate, appressed ascending; the midrib below with prickles 3.5–4 mm long, 22–28 mm apart, stout subulate, ascending; on the subulate apex the margins and midrib below with subulate-serrulations 0.3–0.5 mm long, 4–10 mm apart; pistillate inflorescence terminal, arching, bearing one syncarp; peduncle 27 cm long, 13–20 mm in diameter, 3-sided, leafy bracted; syncarp 23 cm long, 17.5 cm in diameter, ellipsoid-subglobose, bearing 67 phalanges, the ripe core soft and fleshy and quickly shrivelling to a very small remnant; phalanges 5.5–6.2 cm long, the upper half 3.2–4 cm wide, 2.5–3.5 cm thick, oblong-ellipsoid or obovoid, below orange-red, above greenish changing to pink, 5–6-angled, the sides smooth, a little shiny, gently curved, lateral sutures usually none, rarely 1 (–2), the apex convex; central apical sinuses 0.7–2 mm deep, V-shaped at the very bottom, mostly straight; lower half of phalange 3.3–4.2 cm wide, 2.8–3.9 cm thick, fleshy enlarged, pinkish orange, cuneate-oblong in outline, the shoulders 3–6 mm wide, often eaten by small, black ants, and reduced to white scars, 5–8-angled, the sides

smooth, gently curved, the flesh sweet, inoffensive, but not eaten; carpels 4–7, the central ones about $\frac{2}{3}$ as large as the marginal, the apices very low conic, the marginal ones asymmetric and some of them having just distal of the stigma a slight flat platform or even a concavity; stigmas 2.5–4 mm long, from cordate to deltoid or reniform, light brown, papillose, creased, oblique, centripetal; proximal sinus running $\frac{1}{2}$ – $\frac{2}{3}$ way to valley bottom; endocarp slightly suprmedian, bony, mahogany-colored, the inner surfaces shining, the lateral walls 5 mm thick; seeds 12–15 mm long, 5 mm in diameter, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern with a few fibers but filled with aerenchyma of white medullary membranes; basal mesocarp fibrous and fleshy, extensive.

DESCRIPTION OF STAMINATE TREE: Tree 7 m tall, 12 cm in diameter; bark brown, muricate; prop roots none, but tree abused; leaves 1.23 m long, 3.9–4 cm wide, coriaceous, furrowed above the midrib, the sides not plicate, at midsection with 35 secondary parallel veins in each half, no tertiary cross veins, sword-shaped, tapering into a 15–20 cm subulate trigonous apex, this 10 cm down, 3 mm wide; at 3–4.5 cm from the base the margins with prickles 4–5 mm long, 7–21 mm apart, arcuate subulate, with thickened base, ascending; the midrib below beginning at 6–7 cm with prickles 3–4.5 mm long, 4–22 mm apart, similar but reflexed; at midsection the margins with prickles 1.5–2.5 mm long, 6–12 mm apart, subulate, closely appressed ascending; the midrib below with prickles 1.5–2 mm long, 13–25 mm apart, subulate, arcuate ascending; the subulate apex with margins and midrib below with prickles 0.5–0.7 mm long, 3–7 mm apart, subulate-serrations; staminate inflorescence single, terminal, arcuate and pendent, 50 cm long; peduncle fleshy and soon disintegrating; lower bracts with lower part and the other bracts all white; lowest floral bract 48 cm long, 2.2 cm wide, the body ligulate except at base with marginal prickles 2–2.5 mm long, acerose, ascending, closely appressed, white; the apex 20–25 cm long, subulate, foliaceous; median bract 19 cm long, 2.6 cm wide, linear-lanceolate, unarmed except near the tip; spikes about 12, dense, 2.5–4 cm long, 1.5–2 cm in diameter,

cylindric; staminate flowers very numerous, 1.5–1.9 cm long; column 4–8 mm long, bearing a common section of equal length and with about 24 stamens, the free filament tips 1–2 mm long; anther body 2.4–3.6 mm long, linear-lanceolate, bearing an apical subulate prolongation of the connective 0.6–0.7 mm long.

HOLOTYPE: Malaya, Penang Island, 5 miles n. of George Town, top of sea beach, June 30, 1960, *H. St. John* 26,371 (BISH).

SPECIMENS EXAMINED: Malaya, Penang Island, Tanjong Tokong, 6 miles n. of George Town, top of sea beach, staminate, June 30, 1960, *H. St. John* 26,370 (BISH); Penang Island, Mt. Pleasure, 8 miles n. of George Town, top of quartz sand sea beach, clump with stems cut back to 1 m. by 10 cm, old phalanges from the ground, June 30, 1960, *H. St. John* 26,369 (BISH).

DISCUSSION: *P. albibracteatus* is a member of the section *Pandanus*, as is its closest relative, the Singapore species *P. Boryi* Gaud., which has the phalanges with the central apical sinuses 1.5–2.5 mm deep; marginal carpels with a visor projecting over the stigma; leaves 3.5–4.4 cm wide, sword-shaped, at midsection with 39 secondary parallel veins in each half, and near the base the margins with prickles 3–4.5 mm long, 7–25 mm apart. *P. albibracteatus* has the phalanges with the central apical sinuses 0.7–2 mm deep; stigmas lacking a visor; leaves 5–5.5 cm wide, the lower half ligulate, the outer half sword-shaped, secondary parallel veins 41–44 at midsection in each half, near the base the margins with prickles 4.5–7 mm long and 10–45 mm apart.

The new epithet is formed from the Latin words *albus*, white; *bracteatus*, with bracts, and given in allusion to the white floral bracts.

Pandanus ambiglaucus sp. nov. (sect. *Pandanus*)

Figs. 156, 170b

DIAGNOSIS HOLOTYPE: Arbor juvenalis, trunco erecto 1 m alto 10 cm diametro, radicibus futuosis ad 1 m longis et 4 cm diametro brunneis in lineis sparse muriculatis, foliis 2–2.47 m longis 5.8–6.3 cm latis coriaceis viridibus et glaucis in lateribus ambis, spinis omnibus albis, lamina late sulcata et dimidiis subsigmoi-

deis in sectione mediali cum 44–46 nervis parallelis secundariis in quoque dimidio, nervis tertialis nullis, gladiformatis sensim in apice trigono subulato caudato 20–30 cm longo diminuentibus eo 10 cm ex apice 1.8 mm lato, basi amplexicauli et inermi sed ex 5–6 cm marginibus cum aculeis 4–6 mm longis 5–26 mm separatis valde subulatis arcuatis adscendentibus, midnervo infra ex 7.5–8.5 cm cum aculeis 3–4.5 mm longis 20–32 mm separatis arcuatis subulatis reflexis basibus crassis, in sectione mediali marginibus cum aculeis majoribus 2.5–3 mm longis 18–30 mm separatis arcuatis subulatis adscendenti-adpressis basibus crassis plerumque alternantibus cum aculeis minoribus 1–2 mm longis, midnervo infra cum aculeis 1.5–2 mm longis 13–24 mm separatis subulatis adscendentibus, in apice subulato marginibus et midnervo infra cum subulato-serrulis 0.3–1 mm longis 3–8 mm separatis, inflorescentia foeminea terminali arcuati, pedunculo 40 cm longo 2 cm diametro trigono folioso-bracteato cum syncarpio solitario eo 21 cm longo 16 cm diametro ellipsoideo (submaturo et viridi) cum 85 phalangibus eis 6–6.6 cm longis 2.8–4 cm latis 2.8–3.6 cm crassis obovoideis ad apicem infra cuneatis, apice convexo 5–6-anguloso lateribus supra convexis infra concavis (evidente immaturis), laevibus lucidis, suturis lateralibus nullis, sinibus apicalibus centralibus 0.5–2.5 mm profundis latis et vadosis rectis vel subcurvatis, carpelis 7–8 eis centralibus $\frac{1}{2}$ – $\frac{2}{3}$ tam grandibus quam illis marginalibus eis basalibus medialisque cum apicibus subplanis sed illis centralibus cum apicibus oblato-conicis, stigmatibus 2–3 mm longis suborbicularibus vel ellipticis obscure brunneis obliquis sulcatis centripetalibus, ceteris marginalibus truncatis, sinibus proximalibus $\frac{1}{2}$ ad fondam extentis, endocarpio in parte $\frac{1}{3}$ infera osseoso brunneo, seminibus 12–16 mm longis ellipsoideis, mesocarpio supero in quaque carpella cavernam cum fibris et membranis pallidis medullosis formanti, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Young tree, trunk erect 1 m tall, 10 cm in diameter; prop roots up to 1 m long and 4 cm in diameter, sparsely muriculate in vertical lines, brown; leaves 2–2.47 m long, 5.8–6.3 cm wide, coriaceous, green and glaucous on both sides, the spines all white,

the blade broad furrowed over the midrib, the sides slightly sigmoid, at midsection with 44–46 secondary parallel veins in each half, no visible tertiary cross veins, sword-shaped, gradually tapering upwards into a 20–30 cm caudate, subulate, trigonous apex, this 10 cm down 1.8 mm wide, the base amplexicaul and unarmed, but beginning at 5–6 cm up the margins with prickles 4–6 mm long, 5–26 mm apart, stout subulate, arcuate, ascending; the midrib below beginning at 7.5–8.5 cm with prickles 3–4.5 mm long, 20–32 mm apart, arcuate subulate, heavy based, reflexed; at midsection the margins with larger prickles 2.5–3 mm long, 18–30 mm apart, arcuate subulate, heavy based, ascending appressed, mostly alternating with smaller ones 1–2 mm long; the midrib below with prickles 1.5–2 mm long, 13–24 mm apart, subulate, ascending; on the subulate apex the margins and midrib below with subulate serrulations 0.3–1 mm long, 3–8 mm apart; pistillate inflorescence terminal, arching; peduncle 40 cm long, 2 cm in diameter, 3-sided, leafy bracted, bearing a single syncarp, this 21 cm long, 16 cm in diameter, ellipsoid, slightly immature and still green, bearing 85 phalanges, these 6–6.6 cm long, 2.8–4 cm wide, 2.8–3.6 cm thick, obovoid above, cuneate below, the apex convex, 5–6-angled, the sides convex above, concave below (but this probably due to immaturity), smooth, shining; lateral sutures none; central apical sinuses 0.5–2.5 mm deep, shallow, the line straight or gently curved; carpels 7–8, the central ones $\frac{1}{2}$ – $\frac{2}{3}$ as large as the marginal ones, the basal and median phalanges with the carpel apices almost flat, but those near the center with the apices oblate conic; stigmas 2–3 mm long, suborbicular to elliptic, dark brown, oblique, creased, centripetal, some of the marginal ones truncate; proximal sinus running $\frac{1}{2}$ way to valley bottom; endocarp in lower $\frac{1}{3}$, bony, brown; seeds 12–16 mm long, ellipsoid; upper mesocarp forming in each carpel apex a cavern, with fibers and pale medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Singapore, Woodlands Road, 14 miles mark, opposite Kranji Nature Reserve, fresh water swamp, with *Dicranopteris linearis*, July 10, 1960, H. St. John 26,376 (BISH).

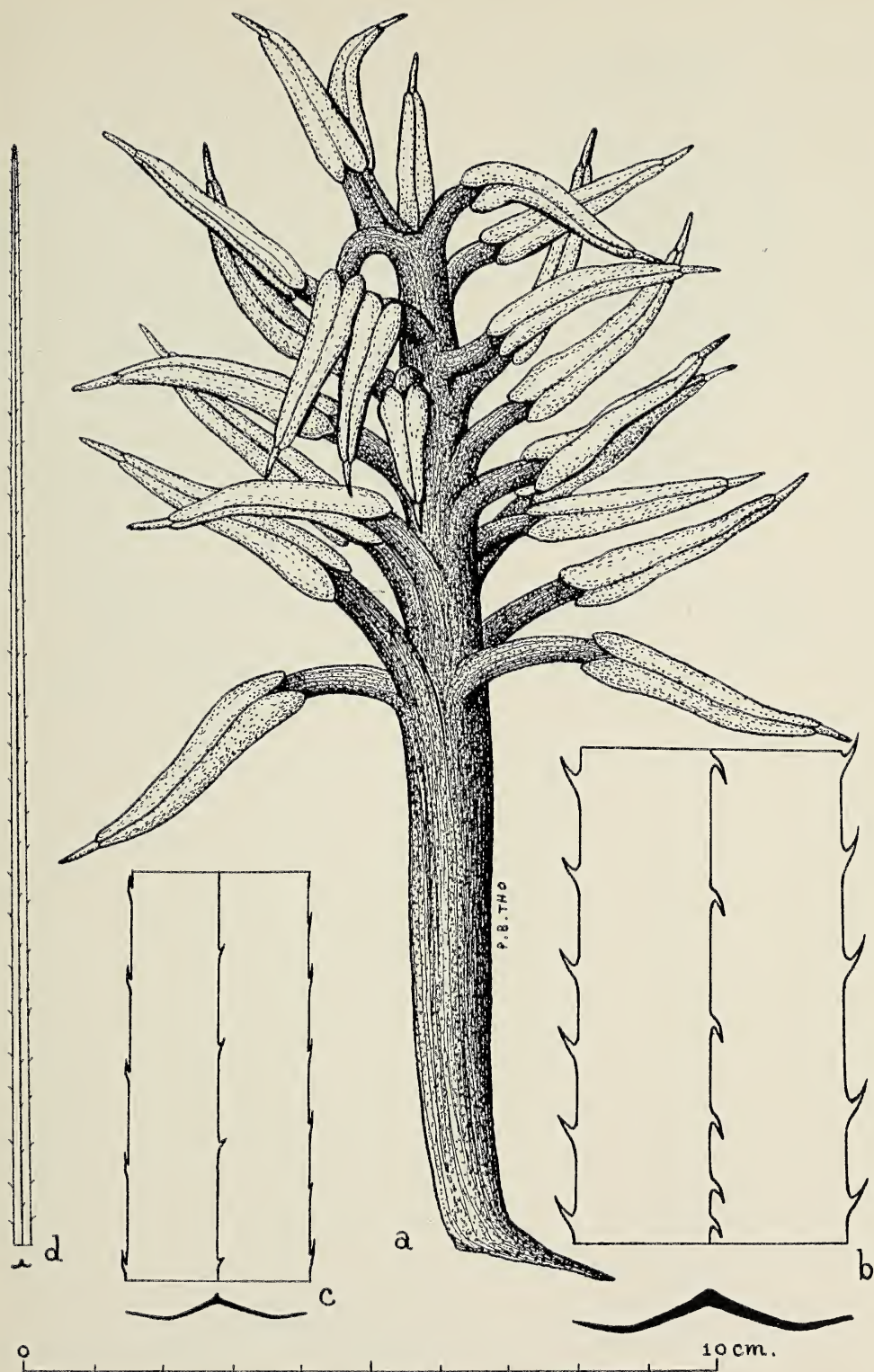


FIG. 155. *Pandanus albibracteatus* St. John, from *St. John* 26,370. *a*, Staminal column with anthers, lateral view, $\times 10$; *b*, leaf base, lower side, $\times 1$; *c*, leaf middle, lower side, $\times 1$; *d*, leaf apex, lower side, $\times 1$.

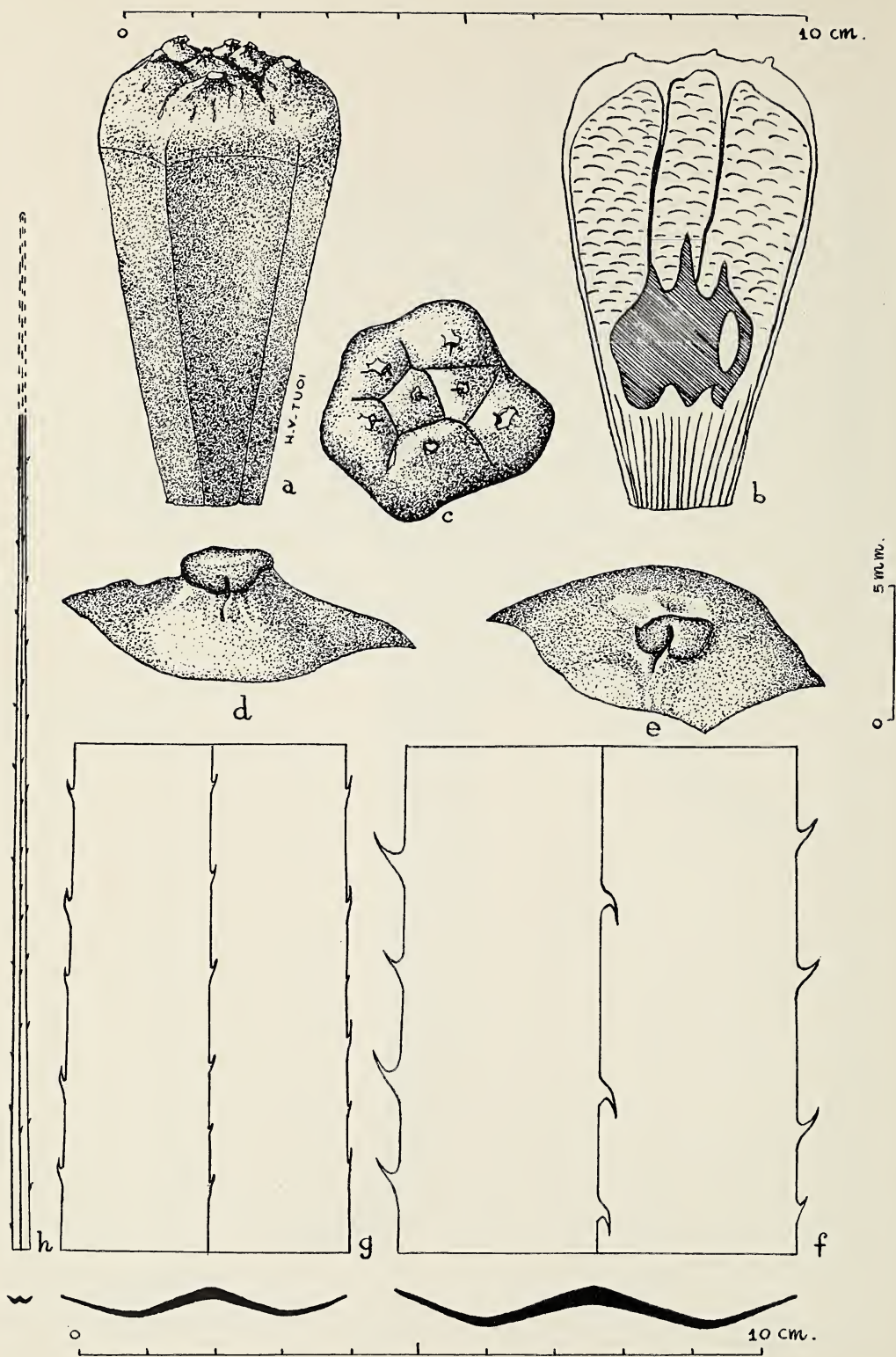


FIG. 156. *Pandanus ambiglaucus* St. John, from holotype. *a*, Phalange, lateral view, $\times 1$; *b*, phalange, longitudinal median section, $\times 1$; *c*, phalange, apical view, $\times 1$; *d*, carpel apex, stigma, and proximal sinus of a median phalange, oblique view, $\times 1$; *e*, carpel apex, stigma, and proximal sinus of a phalange near the base, oblique view, $\times 1$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$; *h*, leaf apex, lower side, $\times 1$.

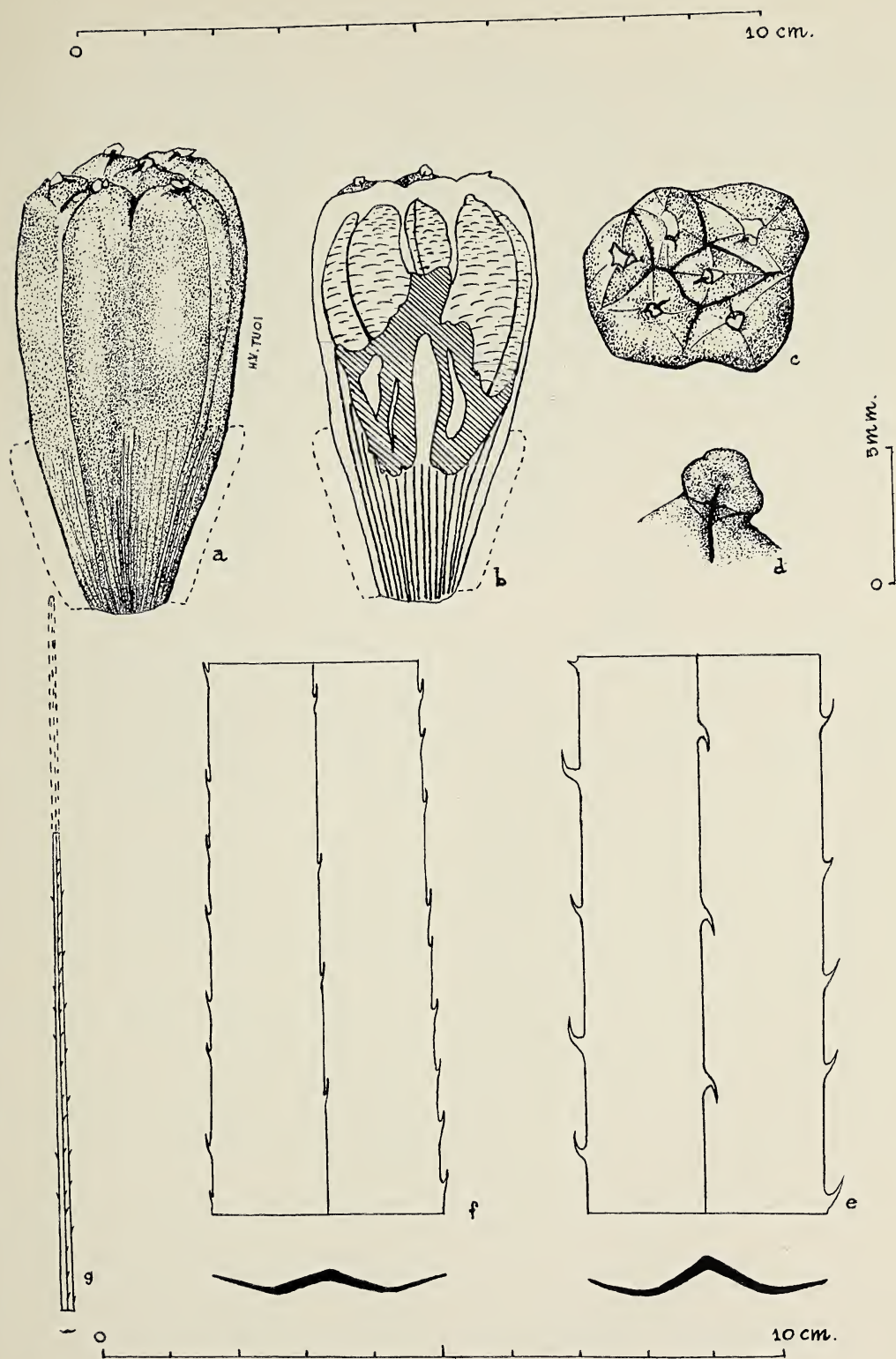


FIG. 157. *Pandanus Boryi* Gaud., from Singapore, Fosberg 36,919. *a*, Phalange, lateral view, $\times 1$; *b*, phalange, longitudinal median section, $\times 1$; *c*, phalange, apical view, $\times 1$; *d*, carpel apex, stigma, and proximal sinus, oblique view, $\times 1$; *e*, leaf base, lower side, $\times 1$; *f*, leaf middle, lower side, $\times 1$; *g*, leaf apex, lower side, $\times 1$.

DISCUSSION: *P. ambiglaucus* is a member of the section *Pandanus*, as is *P. inclinatus* St. John, also of Singapore, its closest relative, and a species with the syncarp with 44–61 phalanges, these with the apex truncate or subtruncate, and the lower half fleshy enlarged; endocarp median; leaves 1.5–1.7 m long, 4.4–4.7 cm wide, above dark olive green, below green; and the secondary veins at midsection 38–40 in each half. *P. ambiglaucus* has the syncarp with 85 phalanges, these with the apex convex, and the lower half cuneate; endocarp in the lower $\frac{1}{3}$; leaves 2–2.47 m long, 5.8–6.3 cm wide, green and glaucous on both sides; and the secondary veins 44–46 in each half at the midsection of the leaf.

The new epithet is from the Greek words *ambos*, both; *glaukos*, color of the sea, applied to the glaucous coating on both sides of the leaves.

Pandanus Boryi Gaud., Bot. Voy. La Bonite, pl. 22, f. 15, 1841

Fig. 157

Description from *Fosberg* 36,919, Singapore: "Small tree," leaves more than 1.64 m long, 3.5 cm wide, subcoriaceous, green above and below, channeled above the midrib, 2-pleated, in section M-shaped, at midsection with 39 parallel secondary veins in each half, no tertiary cross veins, sword-shaped, tapering gradually to the trigonous subulate tip, more than 15 cm long, and about 10 cm down, only 2.5 mm wide, the base amplexicaul and unarmed, but beginning at 4–7 cm the margins with prickles 3–4.5 mm long, 7–25 mm apart, arcuate, subulate, ascending, pale; the midrib below beginning at 19 cm with prickles 3 mm long, 25–40 mm apart, similar but reflexed; at midsection the margins with prickles 2–2.5 mm long, 8–15 mm apart, arcuate subulate, ascending appressed; the midrib below bearing similar prickles 1.7–2 mm long; on the subulate apex the margins and midrib below with serrulations 0.3–0.5 mm long, 3–8 mm apart, red-tipped. "...fruiting head small cylindric, red when ripe"; phalange 6.3 cm long, 3.4 cm wide, 2.8 cm thick, pyriform, compressed, when dried the apex brown, but yellowish below, the sides smooth, shining, gently curved, free in

upper $\frac{1}{3}$, the apex low convex, lateral sutures none (from the direction of the basal fibers and from the remnant of a shoulder, it is apparent that when fresh the basal third had fleshy enlargements); central apical sinuses 1.5–2.5 mm deep, broad; carpels 6, the apices very low, depressed pyramidal, the inner ones slightly the smaller; stigmas 2–2.5 mm wide, reniform, dark brown, papillose, centripetal and mostly oblique, some of the marginal ones with the apex truncate by an overhanging visor which terminates a distal concavity; proximal sinus running $\frac{1}{2}$ way to valley bottom; endocarp median, 3 cm long, bony, massive, dark mahogany-colored, the lateral walls 3 mm thick, the inner surfaces shining; seeds 12 mm long, 3–4 mm in diameter, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern with few fibers but filled with aerenchyma of white medullary membranes; basal mesocarp fibrous and fleshy.

EXPANDED DESCRIPTION FROM OTHER SPECIMENS: Branch tips 4.5–5 cm in diameter, brown, with crowded leaf scars; leaves 1–1.64 m long, 3.5–4.5 cm wide, at midsection with 39–45 parallel secondary veins in each half, near the base the marginal prickles 3–5 mm long, those of the midrib below 3–5 mm long; peduncle terminal, 22 cm long, 15 mm in diameter, 3-sided, leafy bracted, bearing a single syncarp, this 16 cm long, 14 cm in diameter, broadly ellipsoid, bearing numerous phalanges; phalanges 5.5–6 cm long, 2–3.4 cm wide, 2–2.8 cm thick, pyriform to wedge-shaped, compressed; carpels 6–10.

STANDARD SPECIMEN: Singapore: edge of "dry" mangrove swamp, April 17, 1956, *F. R. Fosberg* 36,919 (US).

SPECIMENS EXAMINED: Singapore, Sungei Gunong, Feb. 1893, *H. N. Ridley* 5,003 (SING); Singapore, Dec. 15, 1904, *W. Fox* 12,575 (SING).

DISCUSSION: *P. Boryi* Gaud. is a member of the section *Pandanus*. The type specimen is a single phalange in the Paris museum, collected by Gaudichaud, and left without data. It was a misfortune that he abandoned his taxonomic work half done and devoted his last years to morphogenesis, producing lengthy papers that are now forgotten. *P. Boryi* was published with the binomial and with a figure showing a

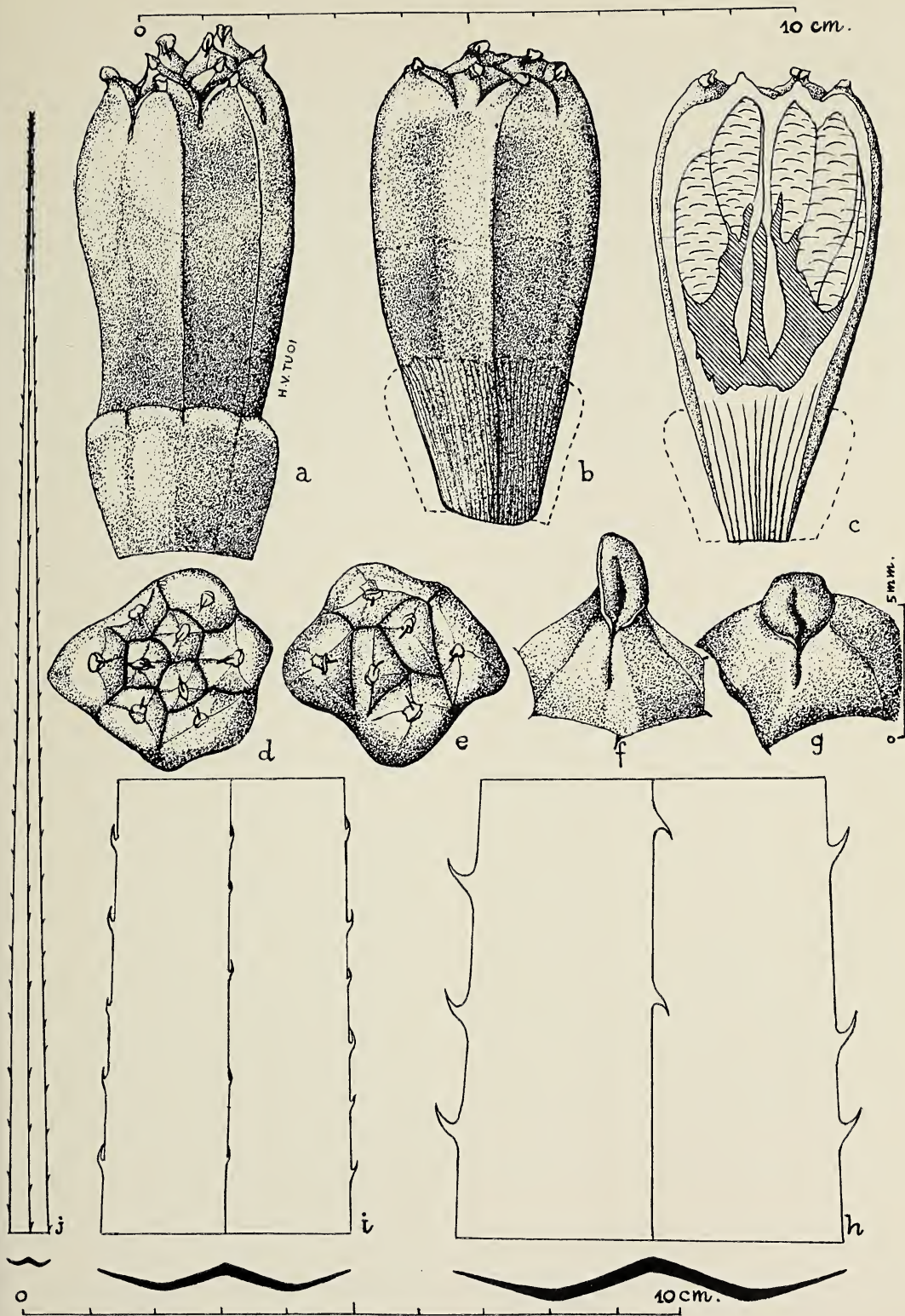


FIG. 158. *Pandanus carnosus* St. John, from holotype. *a*, Fresh lateral phalange, lateral view, $\times 1$; *b*, dried subbasal phalange, lateral view, $\times 1$; *c*, phalange, longitudinal median section, $\times 1$; *d*, lateral phalange, apical view, $\times 1$; *e*, subbasal phalange, apical view, $\times 1$; *f*, apex of carpel in lateral phalange, oblique view, $\times 4$; *g*, apex of carpel in subbasal phalange, oblique view, $\times 4$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$.

lateral view of a phalange, nothing more. Since the genus existed, this was valid publication. Brongniart reviewed the *Pandanus* specimens collected by Gaudichaud and documented them as far as possible (Ann. Sci. Nat. Bot. VI, 1: 290, 1875). For this species he postulated that it came from Ile de la Réunion. However, in the recent detailed revision of the Mascarene species (Linn. Soc. Lond. Bot. Jour. 55: 1-32, 1953) Vaughan and Wiehe found no local species to match it.

It is of interest, then, to note that the recent collection from Singapore, *Fosberg* 36,919, is a perfect match for Gaudichaud's illustration of *P. Boryi*. This collection consists of one phalange and one leaf minus the tip, so it is scarcely more adequate than the Gaudichaud collection. Since it is a perfect match for the Gaudichaud figure, we offer here a description of this phalange and leaf as a standard description to supplement the minimal publication by Gaudichaud. In the Singapore herbarium there are also two collections from Singapore that fall into this same species. One has six phalanges and two leaves minus the tips; the other had a branch, many leaf bases, peduncle, core of the syncarp, and eight phalanges. Together they contribute to our knowledge of the population. No one of them furnishes all the details, but of all, the *Fosberg* 36,919 seems best to take as a standard.

The vessel "La Bonite," on which Charles Gaudichaud was the botanist, circumnavigated the globe in 1836 and 1837, and stopped at Singapore. *Pandanus* is still fairly common on Singapore Island and occurs there in several species. One of the tidal estuaries not far from the harbor is Sungei Pandan, and the general vernacular name of the genus in Malayan is "pandan." This was the source of our generic name, *Pandanus*, latinized and first published by Rumphius, later adopted and made valid by Stickman.

Pandanus carnosus sp. nov. (sect. *Pandanus*)

Fig. 158

DIAGNOSIS HOLOTYPE: Arbor 10 m alta 15 cm diametro, cortice pallide brunneo sparse muricato, radicibus fultrosis 1-2 m longis 3-3.5 cm diametro pallide brunneis in lineis muriculatis, foliis 1.8-2.4 m longis 5-5.2 cm latis supra olivaceo-viridibus et subglaucis infra pallide vir-

idibus coriaceis cum midnervo forti et in centro late sulcatis in sectione mediali cum 45 nervis parallelis secundariis in quoque dimidio nervis tertialis nullis laminis gladiformatis cum apicibus 15-30 cm longis subulatis trigonis eo 10 cm ex apice 0.9-1.3 mm lato basi amplexicaule et inermi sed ex 10 cm marginibus cum spinis 5-6.5 mm longis 11-30 mm separatis valide subulatis arcuatis adscendentibus pallidis, midnervo infra ex 22 cm cum spinis 6 mm longis 15-35 mm separatis simulantibus sed reflexis, in sectione mediali marginibus cum aculeis 3.5-4 mm longis 11-18 mm separatis subulatis valde adpresse adscendentibus apicibus rubris, midnervo infra cum aculeis 3 mm longis 15-25 mm separatis simulantibus adscendentibus, in apice subulato marginibus et midnervo infra cum subulato-serris 0.5-0.8 mm longis 2-11 mm separatis, syncarpio solitario terminali 18 cm longo 15 cm diametro subgloboso cum phalangibus numerosis eis 6.7-7.3 cm longis 2.7-3.5 cm latis 2.4-3.1 cm crassis apice in parte viridi in parte rubro-aurantiaco 5-6-anguloso, parte $\frac{2}{3}$ supera libera oblongo-elliptica vel oblongo-obovoideo apice depresso-convexo lateribus subcurvatis rugulosis sed sublucidis, suturis laterilibus nullis, sinibus centralibus apicalibus 4.5-5.5 mm profundis et V-formatis in apicibus anguste conicis (sed in phalangibus paucis probabiter eis subbasalibus apicibus demissiter pyramidalibus sinibus 2-3.5 mm profundis), carpelis 6-10 apicibus plerumque anguste conicis eis marginalibus $\frac{1}{3}$ latioribus asymmetricalibus et plus minusve distaliter compressis erectis vel subdivergentibus, parte $\frac{1}{3}$ infera phalangis carnosio-incrassata 3-4 mm et deinde 25-35 mm diametro, stigmatibus 3-3.5 mm longis ellipticis sulcatis brunneis papillosis, sinibus proximalibus $\frac{1}{3}$ - $\frac{1}{2}$ ad fondam extensis, endocarpio mediali 2.5-3 cm longo mahogani-brunneo osseoso solido lateribus 3-4 mm crassis intra lucidis, seminibus 13-18 mm longis 4.5 mm diametro fusiformibus, mesocarpio supero in apice carpeli quique cavernam formanti eis lateralibus 2.5 cm longis cum membranibus albis medullosis, mesocarpio basali fibroso et carnosio.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 10 m tall, 15 cm in diameter; bark light brown, sparsely muricate; prop roots 1-2 m long, 3-3.5 cm in diameter, pale brown, muricu-

late in longitudinal lines; leaves 1.8–2.4 m long, 4.4–5.2 cm wide, above olive green and somewhat glaucous, below paler green, coriaceous, with a strong midrib and above it broadly channeled, at midsection with 45 secondary parallel veins in each half, no visible tertiary cross veins, sword-shaped, gradually tapering to the 15–30 cm subulate trigonous apex, this 10 cm down 0.9–1.3 mm wide, the base amplexicaul and unarmed, but beginning at 10 cm the margins with spines 5–6.5 mm long, 11–30 mm apart, stout subulate, arcuate ascending, pale; the midrib below beginning at 22 cm with spines 6 mm long, 15–35 mm apart, similar but reflexed; at midsection the margins with prickles 3.5–4 mm long, 11–18 mm apart, subulate, closely appressed ascending, reddish-tipped; the midrib below with similar ascending prickles 3 mm long, 15–25 mm apart; on the subulate apex the margins and midrib below with subulate-serreae 0.5–0.8 mm long, 2–11 mm apart; syncarp single, terminal, 18 cm long, 15 cm in diameter, subglobose, bearing numerous phalanges, these 6.7–7.3 cm long, 2.7–3.5 cm wide, 2.4–3.1 cm thick, the apex partly green, the remainder red-orange, 5–6-angled, the upper $\frac{2}{3}$ free, oblong-elliptic or oblong-obovoid, the apex low convex, the sides gently curved, rugulose but even so somewhat shining, lateral sutures none; central apical sinuses 4.5–5.5 mm deep and V-shaped when with narrowly conic apices (but on the occasional phalange, probably a subbasal one, with low pyramidal apices, the sinuses only 2–3.5 mm deep); carpels 6–10, the apices usually narrowly conic, the outer ones of the same thickness but about $\frac{1}{3}$ wider, asymmetric and more or less flattened distally, erect or slightly outwardly curved; the lower $\frac{1}{3}$ of phalange fleshy distended with shoulders distended to 3–4 mm all around, thus 25–35 mm in diameter; stigmas 3–3.5 mm long, elliptic, creased, brown, papillose; proximal sinus running $\frac{1}{3}$ – $\frac{1}{2}$ way to valley bottom; endocarp median, 2.5–3 cm long, dull mahogany-brown, bony, massive, the lateral walls 3–4 mm thick, the inner surfaces shining; seeds 13–18 mm long, 4.5 mm in diameter, fusiform; upper mesocarp forming in each carpel apex a cavern, the lateral ones 2.5 cm long, filled with the white membranes of an aerenchyma; basal mesocarp fibrous and fleshy.

HOLOTYPE: Singapore, Kranji village, cut-over thicket near house, 2 m. alt., July 10, 1960, *H. St. John* 26,375 (BISH).

SPECIMENS EXAMINED: Malaya, Pahang, Telok Sisik, Kuantan, near the sea, 4 Dec. 1924, *I. H. Burkill & Md. Haniff* 17,346 (SING).

DISCUSSION: *P. carnosus* is a member of the section *Pandanus*. It is one of the curious Asiatic species with fleshy, enlarged bases of the phalanges. None of the described species are close relatives, but it is related to an undescribed one from Okinawa, represented by the collection *St. John* 25,950.

The new epithet is the Latin adjective *carnosus*, fleshy, in allusion to the fleshy base of the phalange.

Pandanus globosus sp. nov. (sect. *Pandanus*)

Fig. 159

DIAGNOSIS HOLOTYPE: Arbor ? ramis 3 cm diametro brunneis rugosis, foliis 81–90 cm longis 3.5 cm latis supra viridibus infra pallidioribus et apparente glaucis late sulcatis coriaceis in sectione mediali cum 38 nervis parallelis secundariis in quoque medio nervis tertialis nullis laminis gladiformatis sensim in apice 20 cm longo subulato trigono diminuentibus eo 10 cm ex apice 2 mm lato basi amplexicauli inermi sed ex 5 cm marginibus cum aculeis 3.5–5 mm longis 5–12 mm separatis arcuatis subulatis adscendentibus apicibus brunneis, midnervo infra ex 5 cm cum aculeis 2–3 mm longis 6–18 mm separatis simulantibus sed reflexis, in sectione mediali marginibus cum aculeis 2.8–3 mm longis 5–12 mm separatis subulatis valde adpressis adscendentibus, midnervo infra cum aculeis 0.8–1 mm longis 5–12 mm separatis subulatis adscendentibus, in apice subulato marginibus et midnervo infra cum aculeis 0.5–0.8 mm longis 4–8 mm separatis subulatis adpresse adscendentibus, inflorescentia foeminea terminali cum syncarpio solitario, pedunculo 9 cm longo 8 mm diametro trigono folioso-bracteato, syncarpio 8.8 cm diametro globoso cum 26 phalangibus eis 3.6–3.9 cm longis 2.5–2.8 cm latis 2.2–2.5 cm crassis breviter crasse pyriformatis 6-angulosis lateribus planis vel subcurvatis laevibus lucidis in sicco pallide brunneis parte $\frac{2}{3}$ supera libera apice depresso convexo, suturis lateralibus nullis, sinibus apicalibus centralibus 2–3.5 mm pro-

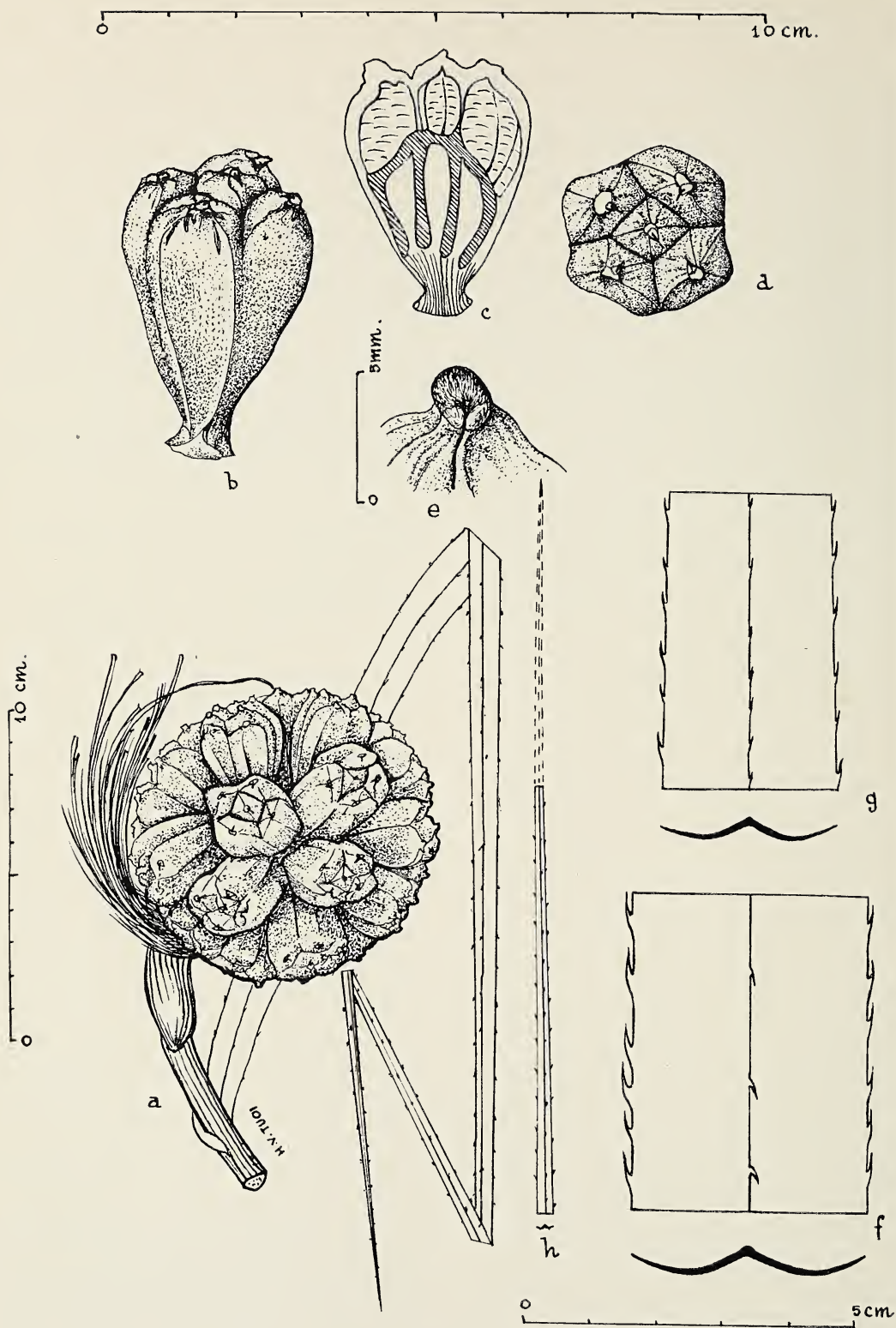


FIG. 159. *Pandanus globosus* St. John, from holotype. *a*, Syncarp, $\times \frac{1}{2}$; *b*, phalange, lateral view, $\times 1$; *c*, phalange, longitudinal median section, $\times 1$; *d*, phalange, apical view, $\times 1$; *e*, carpel apex, stigma, and proximal sinus, oblique view, $\times 4$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$; *h*, leaf apex, lower side, $\times 1$.

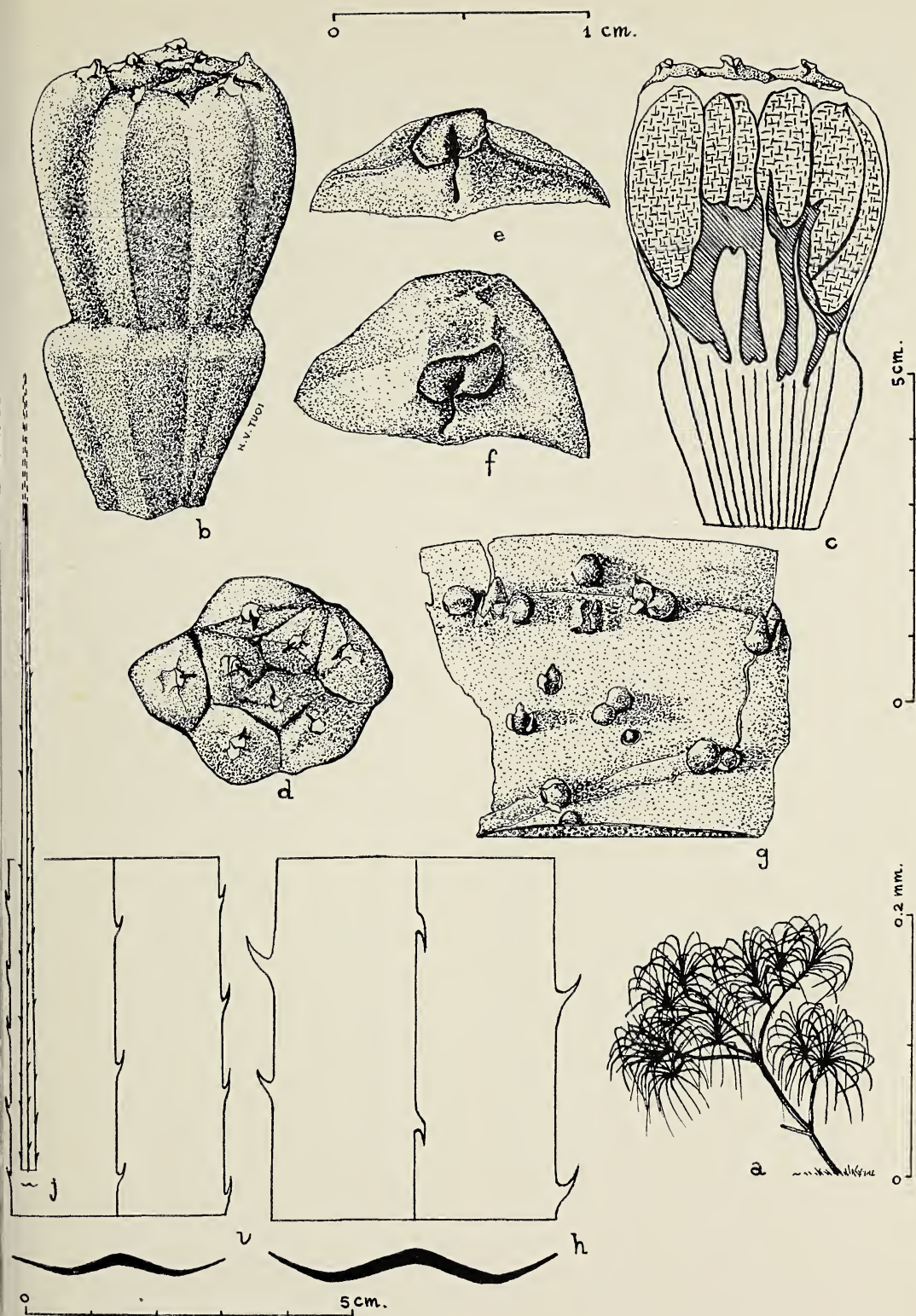


FIG. 160. *Pandanus inclinatus* St. John, from holotype. *a*, Habit, $\times 1/200$; *b*, phalange, lateral view, $\times 1$; *c*, phalange, longitudinal median section, $\times 1$; *d*, phalange, apical view, $\times 1$; *e*, *f*, carpel apices, stigmas, and proximal sinuses, oblique view, $\times 4$; *g*, bark with adventitious rootlets, $\times 1$.

fundis late V-formatis rectis vel subcurvatis, carpelis 5–6 apicibus conicis angulatis basi rotundato apice rugoso eis centralibus quando sunt minoribus, stigmatibus 2.5–3 mm longis cordato-orbicularibus vel ellipticis brunneis papillois prominentibus obliquis centripetalibus, sinibus proximalibus $\frac{1}{2}$ – $\frac{2}{3}$ ad fondam extentis, endocarpio minime submediali brunneo osseoso lateribus 1.5–2 mm crassis intra obscure brunneis lucidis, seminibus 10–14 mm longis 3.5–4 mm diametro ellipsoideis vel obliquiter ellipsoideis, mesocarpio supero in apice quaque carpellae cavernam cum fibris paucis et membranis pallidis medullosis formanti, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Apparently tree-like; branch 3 cm in diameter, brown, roughened by crowded leaf scars; leaves 81–90 cm long, 3.5 cm wide, green above, below paler green and apparently glaucous, with a broad V-shaped furrow above the midrib, coriaceous, at midsection with 38 secondary veins in each half, no visible tertiary cross veins, sword-shaped, tapering gradually to the 20 cm subulate, trigonous apex, this 10 cm down 2 mm wide, the base amplexicaul, unarmed, but beginning 5 cm up the margins with prickles 3.5–5 mm long, 5–12 mm apart, arcuate subulate, fully ascending, brown-tipped; the midrib below beginning at 5 cm with prickles 2–3 mm long, 6–18 mm apart, similar but reflexed; at midsection the margins with prickles 2.8–3 mm long, 5–12 mm apart, subulate, flat appressed, ascending; the midrib below with prickles 0.8–1 mm long, 5–12 mm apart, subulate, ascending; on the subulate tip the margins and midrib below with subulate, appressed ascending prickles 0.5–0.8 mm long, 4–8 mm apart; pistillate inflorescence terminal, bearing one syncarp; peduncle 9 cm long, 8 mm in diameter, 3-sided, leafy bracted; syncarp 8.8 cm in diameter, globose, bearing about 26 phalanges, these 3.6–3.9 cm long, 2.5–2.8 cm wide, 2.2–2.5 cm thick, short, thick pyriform, 6-angled, the sides plane or gently curved, smooth, shining, when dried light brown, upper $\frac{2}{5}$ free, the apex low convex; lateral sutures none; central apical sinuses 2–3.5 mm deep, wide V-shaped, straight or gently curved; carpels 5–6, the apices with a rounded base and conic, angled, wrinkled tip, the central ones, when present, slightly

the smaller; stigmas 2.5–3 mm long, cordate-orbicular to -elliptic, brown, papillose, prominent, oblique, centripetal; proximal sinus running $\frac{1}{2}$ – $\frac{2}{3}$ way to valley bottom; endocarp slightly inframedian, brown, bony, the lateral walls 1.5–2 mm thick, the inner surfaces polished, dark brown; seeds 10–14 mm long, 3.5–4 mm in diameter, ellipsoid or obliquely so; upper mesocarp forming in the apex of each carpel a cavern with a few fibers and with pale, medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Malaya, Kedah, w. coast, P. Dayang Banting, P[ulau] Langkawi, sea level, on limestone, 27 Nov. 1934, M. R. Henderson 29,153 (SING).

SPECIMENS EXAMINED: Borneo: Karimata groep, Poelau, Karimata, 23/3/1931, *Mondi* 155 (BO).

Celebes: Kota Menado, strand, 31/XII/1894, *Koorders* 18,462 (BO).

DISCUSSION: *P. globosus* is a member of the section *Pandanus*, as is its closest relative, the Vietnamese species *P. subulatus* St. John, a species which has the syncarp suborbicular-ellipsoid, 10–10.5 cm in diameter; carpel apices pyramidal or oblate-pyramidal; stigmas 1.5–2 mm long, black; endocarp supramedian; the leaf apex at the point 10 cm down 3.5 mm wide; the margins near the base with spines 5–6 mm long, ascending at 45°; *P. globosus* has the syncarp globose, 8.8 cm in diameter; carpel apices low convex; stigmas 2.5–3 mm long, brown; endocarp inframedian; leaf apex at the point 10 cm down 2 mm wide; the margins near the base with prickles 3.5–5 mm long, fully ascending.

The new epithet is the Latin adjective *globosus*, spherical, and is given in reference to the spherical head of fruits.

Pandanus inclinatus sp. nov. (sect. *Pandanus*)

Figs. 160, 170c

DIAGNOSIS HOLOTYPE: Arbor 8 m alta 13 cm diametro, cortice pallide brunneo muricato et cum radicillis adventivis adpresse adscendentibus ad 1 cm longis, radicibus fulturosis nullis, foliis 1.5–1.7 m longis 4.4–4.7 cm latis coriaceis supra obscure olivaceo-viridibus infra viridibus spinis omnibus albis cum apicibus brunneis lamina 1-sulcatis et lateribus semirevolutis in sectione

mediali cum 38–40 nervis parallelis secundariis in quoque dimidio, nervis tertialis nullis, lamina gladiformi in apice caudato trigono subulato 15–20 cm longo diminuenti eo 10 cm ex apice 1 mm lato, basi amplexicauli et inermi sed ex 3–7 cm marginibus cum aculeis 3.5–6 mm longis 10–30 mm separatis crassiter subulatis subarcuatis adscendentibus, midnervo infra ex 7–8 cm cum aculeis 3–5 mm longis 20–50 mm separatis crassiter subulatis valde reflexis, in sectione mediali marginibus cum aculeis 3–3.5 mm longis 7–17 mm separatis crassiter subulatis adscendentibus valde adpressis, midnervo infra cum aculeis 2.5–3 mm longis 8–23 mm separatis subulatis adscendentibus, in apice subulato marginibus et midnervo infra cum subulato-serrulis 0.5–1 mm longis 5–10 mm separatis vel in loculis nullis, inflorescentia foeminea terminali cum syncarpio uno, pedunculo 30 cm longo 13–15 mm diametro trigono folioso-bracteato, syncarpio 16–23 cm longo 13–20 cm diametro cum 44–61 phalangiis eis 6–6.8 cm longis, dimidio supero 3.2–4.3 cm lato 2.3–3.7 cm crasso oblongo-obovoideo truncato vel subtruncato aurantiaco-rubro apice subviridi 5–7-anguloso lateribus subcurvatis vel subplanis laevibus et lucidis, suturis lateralibus nullis, sinibus centralibus apicalibus 0.7–2 mm profundis rectis vel subcurvatis, dimidia infera phalangis turbinata carnosae humeris carnosae 3–6 mm latis carne subsucrato comesto aurantiaco-rubro, carpelibus 6–12 plerumque 7–9 (sed in gemine 18 et phalangio 5.5 cm lato 4.4 cm crasso) interioribus paene minoribus, apicibus planatis sed pauce oblato-pyramidalibus, stigmatibus 2–3 mm longis ellipticis vel late ellipticis obliquis brunneis sulcatis pluribus marginalium truncatis ex plano oblique et cum concavitate parvo distali, sinibus proximalibus profundis $\frac{1}{2}$ – $\frac{2}{3}$ ad fondam extentis, endocarpio 3 cm longo mediali osseoso obscure mahogani-colorato intra lucido lateribus 2.5 mm crassis, seminibus 14–17 mm longis 4–5.5 mm diametro ellipsoideo, mesocarpio supero in quoque carpelo cavernam cum fibris paucis et aerenchyma cum membranis albis formanti, mesocarpio basali fibroso et carnosio.

DIAGNOSIS OF HOLOTYPE: Tree, 8 m tall, 13 cm in diameter; bark light brown, muricate, and with a few appressed ascending rootlets up to 1 cm in length; prop roots none; leaves 1.5–

1.7 m long, 4.4–4.7 cm wide, coriaceous, above dark olive green, below green, the spines all white with minute brown tips, blade broad furrowed above the midrib, the sides down curved, at midsection with 38–40 secondary parallel veins in each half, no tertiary cross veins, sword-shaped, tapering upwards into a 15–20 cm subulate, trigonous, caudate apex, this 10 cm down 1 mm wide, the base amplexicaul and unarmed, but starting at 3–7 cm up the margins with prickles 3.5–6 mm long, 10–30 mm apart, stout subulate, slightly arcuate, ascending; the midrib below beginning at 7–8 cm with prickles 3–5 mm long, 20–50 mm apart, stout subulate, sharply reflexed; at midsection the margins with prickles 3–3.5 mm long, 7–17 mm apart, stout subulate, ascending, closely appressed; the midrib below with prickles 2.5–3 mm long, 8–23 mm apart, subulate, ascending; on the subulate apex the margins and midrib below with subulate serrulations 0.5–1 mm long, 5–10 mm apart or even lacking for distances on the margins; pistillate inflorescence terminal, bearing one syncarp; peduncle 30 cm long, 13–15 mm in diameter, 3-sided, leafy bracted; syncarp 16–23 cm long, 13–20 cm in diameter, bearing 44–61 phalanges, these 6–6.8 cm long, the upper half 3.2–4.3 cm wide, 2.3–3.7 cm thick, oblong-obovoid, truncate or subtruncate, orange-red, the color becoming paler upwards to the partly greenish apex, 5–7-angled, the sides gently curved or almost plane, smooth and shining; lateral sutures none; central apical sinuses 0.7–2 mm deep, the bottom straight or gently curved, V-shaped, then immediately wide flaring; lower half of phalange turbinate above the truncate base, fleshy enlarged, the shoulders 3–6 mm wide, the flesh slightly sweet, nonirritating, orange-red; carpels 6–12, mostly 7–9 (but in a double 18 and this one 5.5 cm wide, 4.4 cm thick), the central ones only slightly the smaller, the apices flattened but perceptibly oblate pyramidal; stigmas 2–3 mm long, elliptic or broadly so, oblique, brown, creased, many of the marginal ones truncate by the visor-like edge of a distal oblique plane terminating in a small concavity; proximal sinus deep, running $\frac{1}{2}$ – $\frac{2}{3}$ way to valley bottom; endocarp median, 3 cm long, bony, dark mahogany-colored, the inner surfaces shining, the lateral wall 2.5 mm thick; seeds

14–17 mm long, 4–5.5 mm in diameter, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern with a few fibers and an aerenchyma of white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Singapore, Kranji Nature Reserve, brackish swamp with *Sonneratia caseolaris*, *Hibiscus tiliaceus*, *Acrostichum aureum*, July 10, 1960, *H. St. John* 26,378 (BISH).

DISCUSSION: *P. inclinatus* is a member of the section *Pandanus*, as is its closest relative, *P. vietnamensis* St. John, of Vietnam, a species with the syncarp 27 cm long, with 106 phalanges, these 5.8–6 cm long, the apex low convex; stigma 3.5–5 mm long or wide, black; leaves 0.99–1.49 m long, 5–6 cm wide, the margin near the base with spines 4–11 mm long, the nearby midrib below with spines 6–8 mm long. *P. inclinatus* has the syncarp 16–23 cm long, with 44–61 phalanges, these 6–6.8 cm long, the apex truncate or subtruncate; stigmas 2–3 mm long, brown; leaves 1.5–1.7 m long, 4.4–4.7 cm wide, the margin near the base with prickles 3.5–6 mm long, and the nearby midrib below with prickles 3–5 mm long.

The new epithet is the Latin participle *inclinatus*, inclined, given in reference to the oblique stigmas.

Pandanus incrassatus sp. nov. (sect. *Pandanus*)

Figs. 161, 171

DIAGNOSIS HOLOTYPE: Arbor 7–8 m alta 8–10 cm diametro, cortice griseo remote muricato in ramis vetustioribus et trunco cum radicillis adventivis paucis adpresse adscendentibus, radicibus fulturosis 5–10 dm longis 10–13 mm diametro pallide brunneis cum radicillis brevibus spiniformatis in lineis, foliis 1.45–1.7 m longis 4.2–4.3 cm latis coriaceis supra olivaceo-viridibus infra viridibus et glaucis spinis albis deinde apicibus brunneis, laminis 1-sulcatis et cum plicis duobus rotundatis in sectione mediali cum 34–35 nervis secundariis in quoque medio nervis tertialis nullis gladiiformatis sensim in apice 30 cm longo subulato trigono diminuentibus eo 10 cm ex apice 1.1 mm lato, basi amplexicauli et inermi albo sed ex 7–9 cm marginibus cum spinis 3.5–5 mm longis 15–25 mm separatis arcuatis crassiter subulatis adscendentibus, midnervo infra ex 9–12 cm cum spinis

3–4 mm longis 20–28 mm separatis valide subulatis reflexis, in sectione mediali marginibus cum aculeis 2.5–3 mm longis 10–20 mm separatis arcuatis subulatis adpresse adscendentibus, midnervo infra cum aculeis 1.5–2 mm longis 12–20 mm separatis arcuatis subulatis adscendentibus, in apice subulato marginibus et midnervo infra cum subulato-serrulis 0.5–0.7 mm longis 3–5 mm separatis, inflorescentia foeminea terminali cum syncarpio solitario pendenti, pedunculo 23 cm longo 1.5 cm diametro trigono folioso-bracteato, syncarpio 15 cm longo 14.5 cm diametro subgloboso cum 54 phalangibus eis 4.6–5.2 cm longis media supera 2.5–3.1 cm longa, 3–3.6 cm lata 2.3–3 cm crassa obovoidea plano-truncata viridi deinde rubro-aurantiaca 5–6-angulosa lateribus subcurvatis infra laevibus et lucidis supra rugulosis et sublucidis, suturis lateralibus nullis, sinibus apicalibus centralibus plerumque (et in phalangibus lateralibus apicalibusque omnibus) 1–2 mm profundis late V-formatis rectis vel subcurvatis (vel in phalangibus subbasalibus paucis 2–3 mm profundis), media infera phalangis carnosio-incrassata 2.8–3.6 cm lata 2.4–3.1 cm crassa, late cuneata supra aurantiaco-rubra infra pallidiori, humeris 2–5 mm latis undulatis carne saccharosa sed non consumpta, carpelis 5–8 centralibus $\frac{1}{2}$ – $\frac{2}{3}$ tam grandibus quam marginalibus, phalangibus dimidii superi cum apicibus carpeli subtruncatis vel oblatiori-pyramidalibus sed eis dimidii inferi cum apicibus oblato-pyramidalibus, stigmatibus 2–3 mm longis ellipsoideis obscure brunneis papillosis sulcatis obliquis prominentibus centripetalibus eis marginalibus plerumque cum supra stigmatem galea distali cartilaginea, sinibus proximalibus $\frac{1}{2}$ – $\frac{2}{3}$ ad fondam extentis, endocarpio 2.5 cm longo mediali osseoso obscure brunneo intra lucido lateribus 2.5 mm crassis, seminibus 12 mm longis 4 mm diametro ellipsoideis, mesocarpio supero in apice quique carpeli cavernam cum membranis albis lucidis medullosis formanti, mesocarpio basali fibroso et carnosio.

DIAGNOSIS OF HOLOTYPE: Tree 7–8 m tall, 8–10 cm in diameter; bark gray, remotely muricate, and the older trunk with a few appressed ascending adventitious rootlets; prop roots 5–10 dm long, 10–13 mm in diameter, light brown, with remote, short, spinelike rootlets in vertical

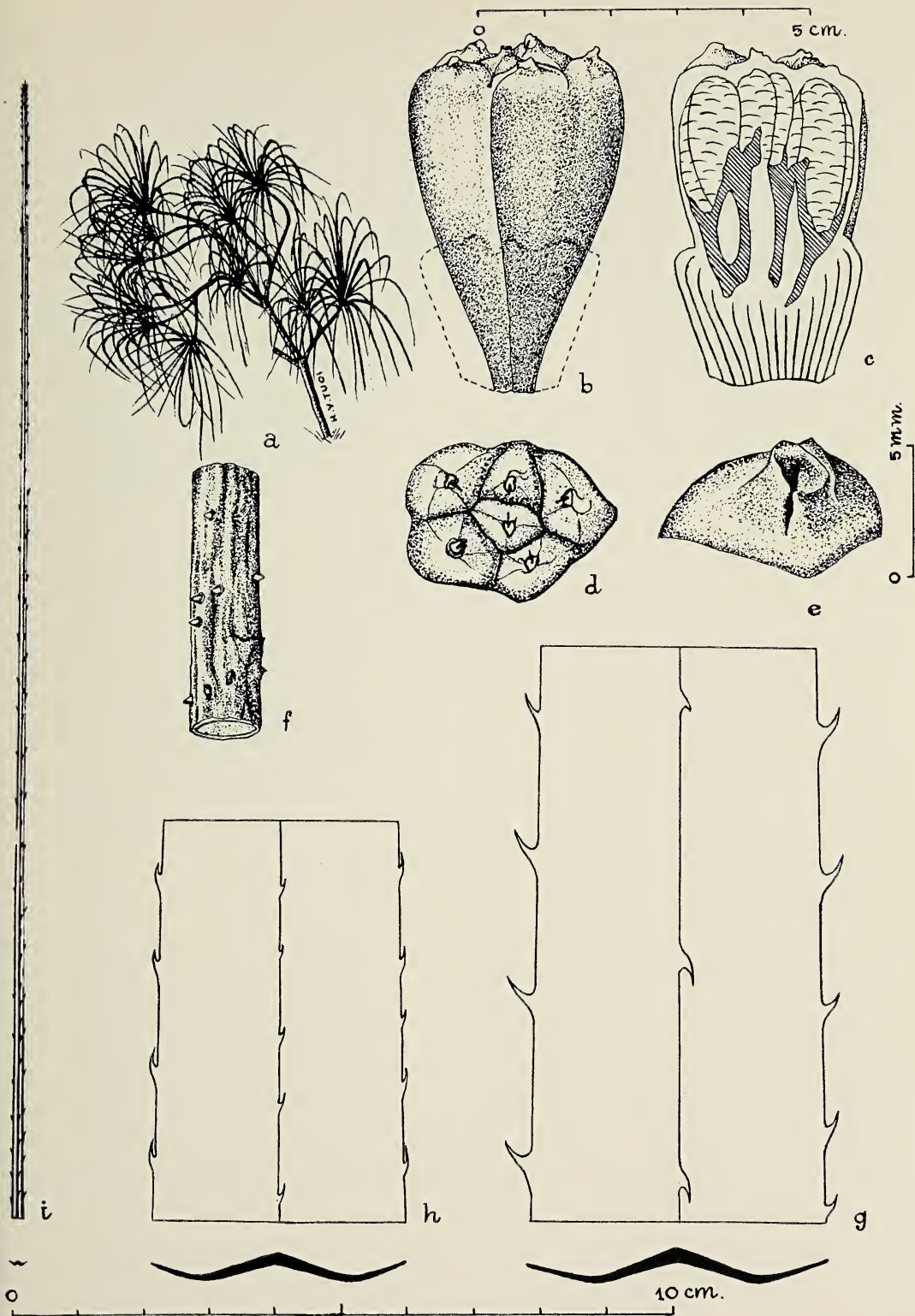


FIG. 161. *Pandanus incrassatus* St. John, from holotype. *a*, Habit, $\times 1/100$; *b*, dried phalange, lateral view, $\times 1$; *c*, phalange, longitudinal median section, $\times 1$; *d*, phalange, apical view, $\times 1$; *e*, carpel apex, stigma, and proximal sinus, oblique view, $\times 4$; *f*, prop root with spinelike rootlets, $\times 1$; *g*, leaf base, lower side, $\times 1$; *h*, leaf middle, lower side, $\times 1$; *i*, leaf apex, lower side, $\times 1$.

rows; leaves 1.45–1.7 m long, 4.2–4.3 cm wide, coriaceous, above olive green, below green and glaucous, the spines white, becoming brown-tipped, 1-ribbed and with two rounded pleats, at midsection with 34–35 secondary parallel veins in each half, no visible tertiary cross veins, sword-shaped, long tapering to a 30 cm subulate, trigonous apex, this 10 cm down 1.1 mm wide, the base amplexicaul and unarmed, white, beginning at 7–9 cm the margins with spines 3.5–5 mm long, 15–25 mm apart, arcuate, heavy subulate, ascending; the midrib below beginning at 9–12 cm with spines 3–4 mm long, 20–28 mm apart, stout subulate, reflexed; at midsection the margins with prickles 2.5–3 mm long, 10–20 mm apart, arcuate subulate, appressed ascending; the midrib below with prickles 1.5–2 mm long, 12–20 mm apart, arcuate subulate, ascending; near the apex the margins and midrib below with subulate serrulations 0.5–0.7 mm long, 3–5 mm apart; pistillate inflorescence terminal, bearing 1 pendent syncarp; peduncle 23 cm long, 1.5 cm in diameter, 3-sided, leafy-bracted; syncarp 15 cm long, 14.5 cm in diameter, subglobose, bearing 54 phalanges, these 4.6–5.2 cm long, the upper half 2.5–3.1 cm long, 3–3.6 cm wide, 2.3–3 cm thick, obovoid, flat truncate, green, turning red-orange, the shade deepening downwards, 5–6-angled, the sides gently curving, below smooth and shining, above rugulose and less shiny; lateral sutures none; central apical sinuses mostly (that is, for the lateral and apical phalanges) 1–2 mm deep, wide V-shaped, straight or gently curving (on a few subbasal ones 2–3 mm deep); lower half of phalange fleshy enlarged, 2.8–3.6 cm wide, 2.4–3.1 cm thick, wide cuneate, vermilion above, gradually paling below, the shoulders 2–5 mm wide, scalloped; pulp sweetish, innocuous, but not eaten; carpels 5–8, the central 1–2 being $\frac{1}{2}$ – $\frac{2}{3}$ the size of the marginal ones; on the phalanges of the upper half the carpel apices subtruncate or very oblate pyramidal, on those of the lower half the carpel apices oblate-pyramidal; stigmas 2–3 mm long, ellipsoid, dark brown, papillose, creased, oblique, prominent, centripetal, the marginal ones mostly with a distal, cartilaginous visor partly projecting over the stigma; proximal sinus running $\frac{1}{2}$ – $\frac{2}{3}$ way to valley bottom; endocarp median

2.5 cm long, bony, dark brown, the inner surfaces shining, the lateral walls 2.5 mm thick; seeds 12 mm long, 4 mm in diameter, ellipsoid; upper mesocarp forming a cavern in each carpel apex with white, shining, medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Singapore, Kranji Nature Reserve, mangrove swamp, with *Sonneratia caseolaris*, *Hibiscus tiliaceus*, *Acanthus ilicifolius*, near sea level, 7 July 1960, H. St. John 26,374 (BISH).

DISCUSSION: *P. incrassatus* is a member of the section *Pandanus*, as is its closest relative, the Vietnamese species *P. reversispiralis* St. John, a species with the syncarp oval-subglobose; phalanges 4.3–4.6 cm long, orange, the apex low convex; stigmas all terminal, exposed; leaves 70–130 cm long, 4.8–6 cm wide, slightly glaucous above, at midsection the margins with prickles 3–4 mm long. *P. incrassatus* has the syncarp subglobose; phalanges 4.6–5.2 cm long, red-orange, the apex truncate; marginal stigmas covered by a visor; leaves 145–170 cm long, 4.2–4.3 cm wide, olive green, not glaucous above, and at midsection the margins with prickles 2.5–3 mm long.

The new epithet is the Latin adjective *incrassatus*, thickened, and is given with allusion to the thickened base of the phalange.

Pandanus obtusus sp. nov. (sect. *Pandanus*)

Fig. 162

DIAGNOSIS HOLOTYPI: Arbor ? foliis 85–88 cm longis 3.4 cm latis coriaceis 1-sulcatis lateribus arcuatis in sectione mediali cum 37–39 nervis parallelis secundariis in quoque medio eis infra conspicuis, nervis tertialis nullis, laminis gladiformatis sensim in apice 15 cm longo subulato trigono diminuentibus eo 10 cm ex apice 2.5 mm lato, basi amplexicauli et inermis ex 5 cm marginibus cum aculeis 2.5–4 mm longis 8–14 mm separatis arcuatis subulatis pallidis in 45° adscendentibus, midnervo infra ex 8.5 cm cum aculeis 3.5–4 mm longis 12–20 mm separatis subulatis valde reflexis basibus crassiter conicis, in sectione mediali marginibus cum aculeis 3–3.5 mm longis 6–11 mm separatis arcuatis subulatis adscendentibus apicibus rubris, midnervo infra angusto salienti cum aculeis 1.5–2 mm longis 7–10 mm separatis arcu-

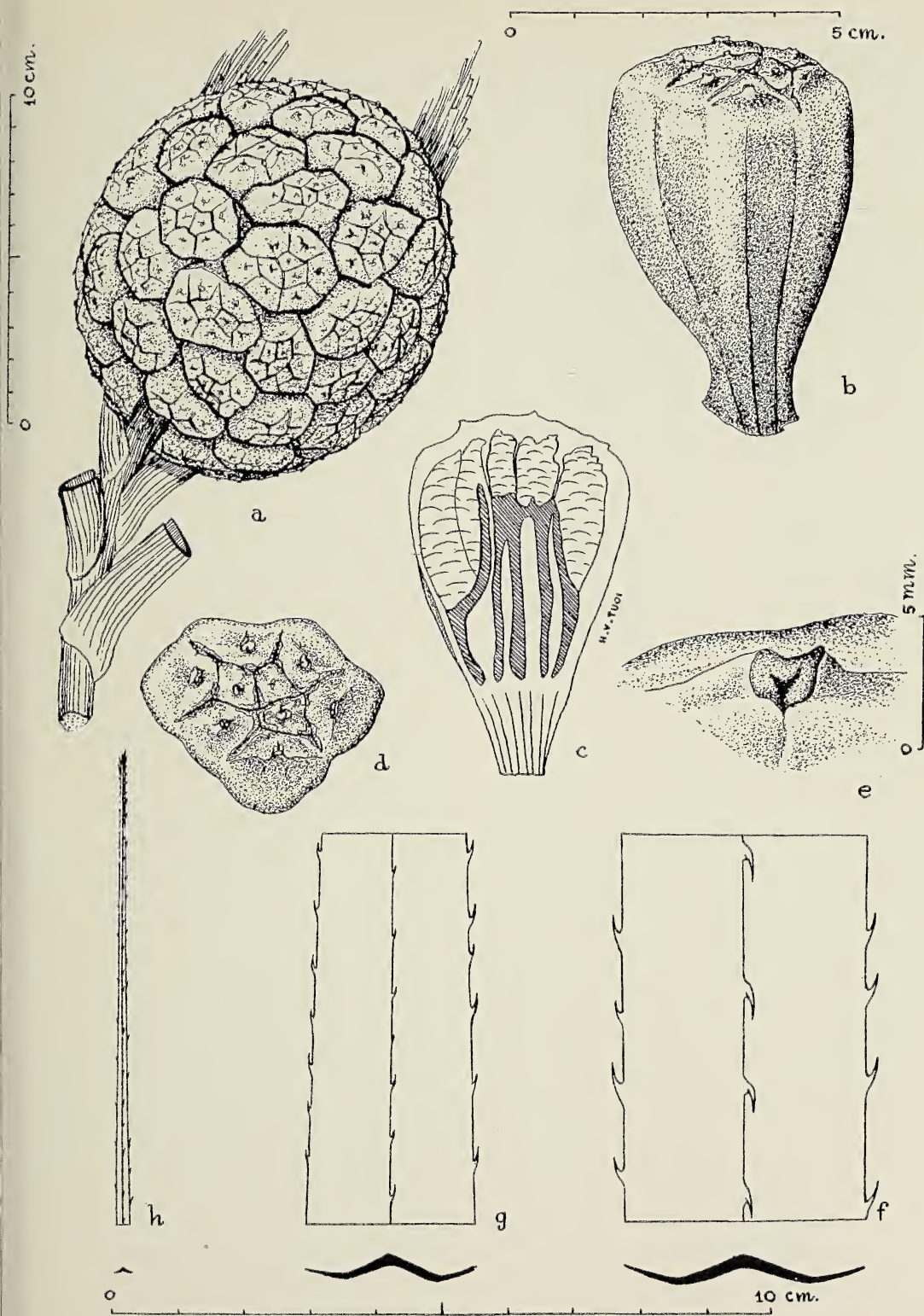


FIG. 162. *Pandanus obtusus* St. John, from holotype. *a*, Syncarp, $\times \frac{1}{2}$; *b*, phalange, lateral view, $\times 1$; *c*, phalange, longitudinal median section, $\times 1$; *d*, phalange, apical view, $\times 1$; *e*, carpel apex, stigma, and proximal sinus, oblique view, $\times 4$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$; *h*, leaf apex, lower side, $\times 1$.

atis subulatis adscendentibus, in apice subulato marginibus et midnervo infra cum subulato-serrulis 0.3–0.7 mm longis 3–7 mm separatis, inflorescentia foeminea cum syncarpio unico terminali, pedunculo 23 cm et plus longo clavato in apice 11 mm diametro subtrigono, syncarpio globoso ? 12 cm diametro cum circa 38 phalangibus eis 5–5.5 cm longis 3–3.8 cm latis 2.7–3.3 cm crassis cuneatis 5–6-angulosis in sicco pallide brunneis lateribus laevibus lucidis subcurvatis vel subplanis parte $\frac{1}{3}$ supra libera apice convexo vel alte convexo suturis laterilibus nullis, sinibus centralibus apicalibus olim lineas brunneas, carpelis 8–10 apicibus rotundatis interioribus minoribus et $\frac{1}{2}$ tam grandibus quam marginalibus, stigmatibus 2–2.5 mm longis cordatis vel reniformibus obliquis centripetalibus, sinibus proximalibus brevibus $\frac{1}{3}$ – $\frac{1}{4}$ ad fondam extentis, endocarpio mediali 2.5–3 cm longo osseoso extra brunneo intra pallidi lateribus 2 mm crassis, seminibus 12 mm longis 3.5 mm diametro obliquiter ovoideis, mesocarpio supero in apice carpello quoque cavernam formanti eis lateralibus majoribus cum fibris longitudinalibus et membranis albis medullosis, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Probably treelike; leaves 85–130 cm long, 3.4 cm wide, coriaceous, furrowed above the midrib, the two halves gently arching, at midsection with 21–39 secondary parallel longitudinal veins in each half, these conspicuous below, no visible cross veins, blade swordlike, tapering upwards and gradually narrowed to a 15 cm subulate, trigonous apex which 10 cm down is 2.5 mm wide, the base amplexicaul and unarmed, but beginning at 5 cm the margins with prickles 2.5–4 mm long, 8–14 mm apart, arcuate subulate, pale, ascending at 45°; the midrib below beginning at 8.5 cm with prickles 3.5–4.5 mm long, 12–20 mm apart, the base heavy conic, the rest subulate, fully reflexed; at midsection the margins with prickles 3–3.5 mm long, 6–11 mm apart, arcuate subulate, ascending, reddish-tipped; the midrib below narrow and salient, with prickles 1.5–2 mm long, 7–10 mm apart, arcuate subulate, ascending; on the subulate apex the margins and midrib below with subulate-tipped serrations 0.3–0.7 mm long, 3–7 mm apart; pistillate inflorescence

with a single, terminal syncarp; peduncle more than 23 cm in length, clavate and at apex 11 mm in diameter, somewhat 3-sided; syncarp apparently globose and 12 cm in diameter, and bearing about 38 phalanges, these 5–5.5 cm long, 3–3.8 cm wide, 2.7–3.3 cm thick, cuneiform, 5–6-angled, when dried pale brown, the sides smooth and shiny, gently curving or flattish, free in upper $\frac{1}{3}$, the apex convex or high convex, lateral sutures none, central apical sinuses mere brown lines on the obtuse apex; carpels 8–10, the apices rounded, not raised, the inner ones smaller, about $\frac{1}{2}$ the size of the marginal ones; stigmas 2–2.5 mm long, cordate to reniform, oblique, centripetal; proximal sinus a very short crack or hole by the stigma, running $\frac{1}{4}$ – $\frac{1}{3}$ way to the valley bottom; endocarp median, 2.5–3 cm long, bony, pale within, dark brown near the margins, the seed cavities shining, the lateral walls 2 mm thick; seeds 12 mm long, 3.5 mm in diameter, obliquely ovoid; upper mesocarp forming in the apex of each carpel a cavern, the lateral ones thrice the larger, with longitudinal fibers and white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Malaya, Pahang, Beserah, Kuantan, sea level, 18 Aug. 1929, M. R. Henderson 22,746 (SING).

SPECIMENS EXAMINED: Singapore, 15 Feb. 1870, J. S. G[oodenough], (SING). This has leaves only 2 cm wide, and with 21 secondary veins on a side, but the phalanges seem identical.

DISCUSSION: *P. obtusus* is a member of the section *Pandanus*. In that section the most similar species seems to be a Marquesan one, *P. tectorius* Soland. var. *uapensis* F. Br., which has the phalanges 5.4–6 cm long, 4.5 cm wide, the apical and lateral sutures very shallow or superficial; apical central sinuses 1 mm deep; stigmas 3 mm long; endocarp suprmedian, but the leaves and syncarp are unknown. *P. obtusus* has the phalanges 5–5.5 cm long, 3–3.8 cm wide, the lateral sutures none, the apical central sinuses mere tessellate rulings; stigmas 2–2.5 mm long; and the endocarp median.

The new epithet is the Latin word *obtusus*, blunt or obtuse, and is given with reference to the obtuse phalange and carpel apices.

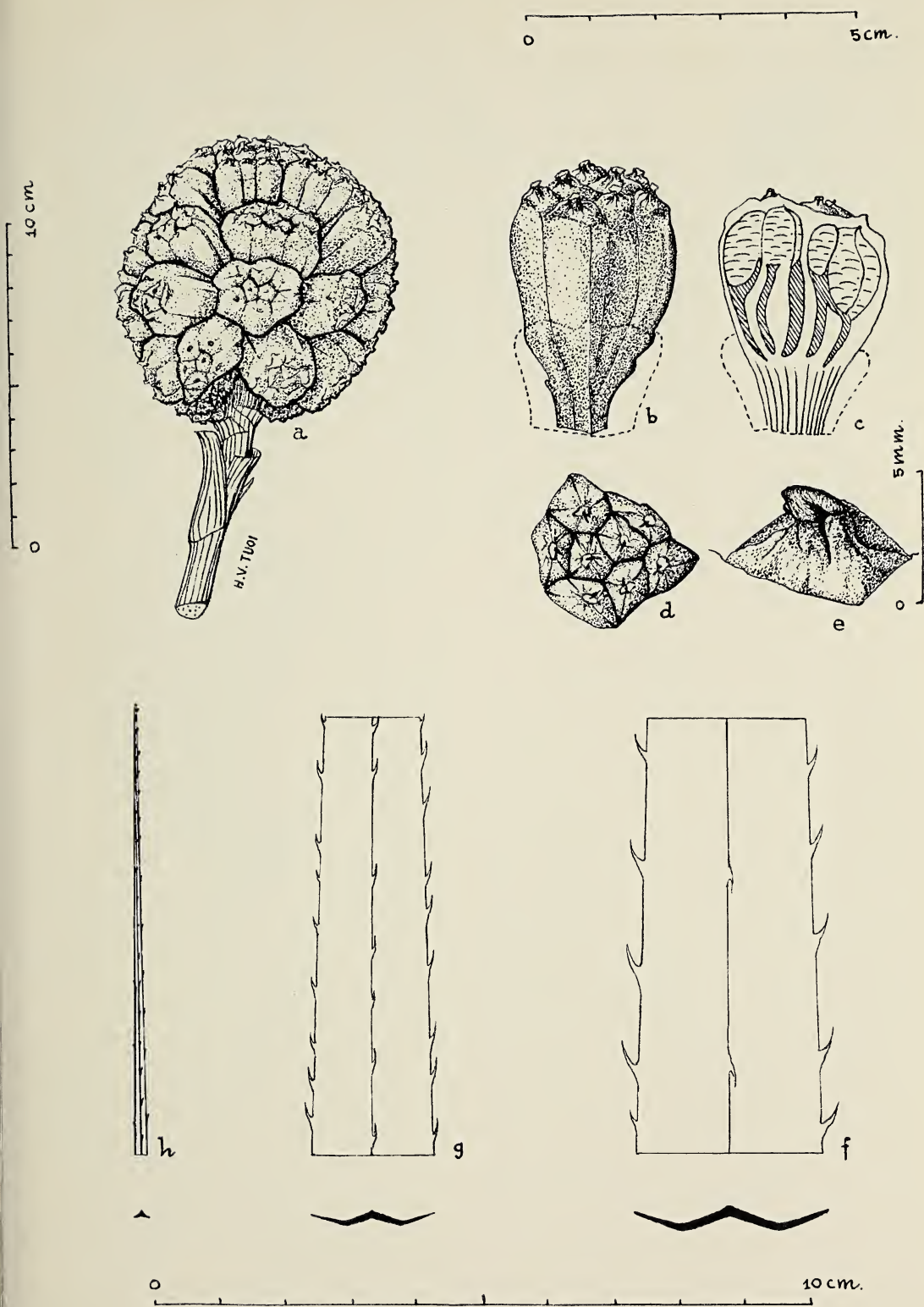


FIG. 163. *Pandanus rubricoloratus* St. John, from holotype. *a*, Syncarp, $\times \frac{1}{2}$; *b*, dried phalange, lateral view, $\times 1$; *c*, phalange, longitudinal median section, $\times 1$; *d*, phalange, apical view, $\times 1$; *e*, carpel apex, stigma, and proximal sinus, oblique view, $\times 4$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$; *h*, leaf apex, lower side, $\times 1$.

Pandanus rubricoloratus sp. nov. (sect. *Pandanus*)

Fig. 163

DIAGNOSIS HOLOTYPE: Arboriformis 3–5 m alta, foliis 66–73 cm longis 2.8–3 cm latis coriaceis supra viridibus infra pallidioribus supra midnervum sulcatis in sectione mediali cum 27 nervis parallelis secundariis in quoque medio nervis tertialis nullis laminis gladiiformatis in apice 12–15 cm longo subulato sensim diminuentibus eo 10 cm ex apice 4 mm lato basi amplexicauli et inermi sed ex 3–4 cm marginibus cum aculeis 2.5–5 mm longis 4–18 mm separatis subulatis pallidis adscendentibus, midnervo infra ex 8–10 cm cum aculeis 2.5–3 mm longis 16–30 mm separatis simulantibus sed adpresse reflexis, in sectione mediali marginibus cum aculeis 2–2.5 mm longis 4–12 mm separatis subulatis adscendentibus apicibus brunneis, midnervo infra cum aculeis simulantibus 1.5–2 mm longis 6–13 mm separatis; in apice subulato marginibus et midnervo infra cum subulato-serrulis 0.6–1 mm longis 2–6 mm separatis; inflorescentia foeminea terminali cum syncarpio solitario, pedunculo 15 cm et plus longo 8 mm diametro exclavatis trigono foliosobracteato, syncarpio 9 cm longo 8.5 cm diametro globoso cum circa 34 phalangibus, eis 3.6 cm longis 2.4–2.7 cm latis 2–2.4 cm crassis rubris parte 5/9 supra libera, hac late ellipsoidea 5–6-angulosa apice depresso convexo lateribus subcurvatis laevibus suturis lateralibus nullis, sinibus apicalibus centralibus 0.5–2 mm profundis vadosis, carpelis 6–9 (in gemine 12 et phalangio 3.3 cm lato) apicibus depresso pyramidalibus angulatis rugosis (in phalangibus basalibus apicibus depresso convexis) parte 4/9 infera carnosio-incrassata, stigmatibus 2–3.5 mm latis cordatis griseis horizontalibus vel obliquis centripetalibus, sinibus proximalibus latis $\frac{1}{2}$ ad fondam extentis, endocarpio mediali 15 mm longo osseoso obscure brunneo lateribus 1.5 mm crassis intra papillosis et sublucidis, seminibus 8–11 mm longis obliquiter ellipsoideis, mesocarpio supero in apice quoque carpelo cavernam cum fibris paucis et membranis brunneis medullosis, mesocarpio basali fibroso et carnosio.

DIAGNOSIS OF HOLOTYPE: Treelike, 3–5 m tall; leaves 66–73 cm long, 2.8–3 cm wide,

coriaceous, green above, paler beneath, furrowed above the strong midrib, the sides arching, at midsection with 27 parallel secondary veins in each half, no tertiary cross veins, blade sword-shaped, tapering upwards and gradually tapering to the 12–15 cm subulate apex which 10 cm down is 4 mm wide, the base amplexicaul and unarmed, but beginning 3–4 cm up the margins with prickles 2.5–5 mm long, 4–18 mm apart, subulate, ascending, pale; midrib below beginning at 8–10 cm with prickles 2.5–3 mm long, 16–30 mm apart, similar but reflexed, appressed; at midsection the margins with prickles 2–2.5 mm long, 4–12 mm apart, subulate, ascending, brown-tipped; the midrib below with similar prickles 1.5–2 mm long, 6–13 mm apart; on the subulate tip the margins and midrib below with subulate serrations 0.6–1 mm long, 2–6 mm apart; pistillate inflorescence terminal, bearing one syncarp; peduncle more than 15 cm long, 8 mm in diameter, not clavate, 3-sided, leafy bracted; syncarp 9 cm long, 8.5 cm in diameter, globose, bearing about 34 phalanges, these 3.6 cm long, 2.4–2.7 cm wide, 2–2.4 cm thick, red, upper 5/9 free, this part broadly ellipsoid, 5–6-angled, the apex low convex, the sides gently curved, smooth, lateral sutures none; central apical sinuses 0.5–2 mm deep, shallow; carpels 6–9 (in a double 12, and the phalange 3.3 cm wide), the apices low pyramidal, angled and wrinkled (on the basal phalanges the carpel apices low convex); lower 4/9 of phalange fleshy enlarged as shown by persistent shoulders; stigmas 2–3.5 mm wide, cordate, gray, horizontal or oblique, centripetal; proximal sinus wide, running $\frac{1}{2}$ way to valley bottom; endocarp median, 15 mm long, bony, blackish brown, the lateral walls 1.5 mm thick, the inner surfaces papillose, a little shiny; seeds 8–11 mm long, oblique ellipsoid; upper mesocarp forming in the apex of each carpel a cavern with a few fibers and an aerenchyma tissue of brownish medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Malaya, Pahang, Pulau Tioman, Telok Paya, sea level, 19 May 1927, M. R. Henderson 18,444 (SING).

DISCUSSION: *P. rubricoloratus* is a member of the section *Pandanus*, as is its closest relative, the Vietnamese species *P. reversispiralis* St.

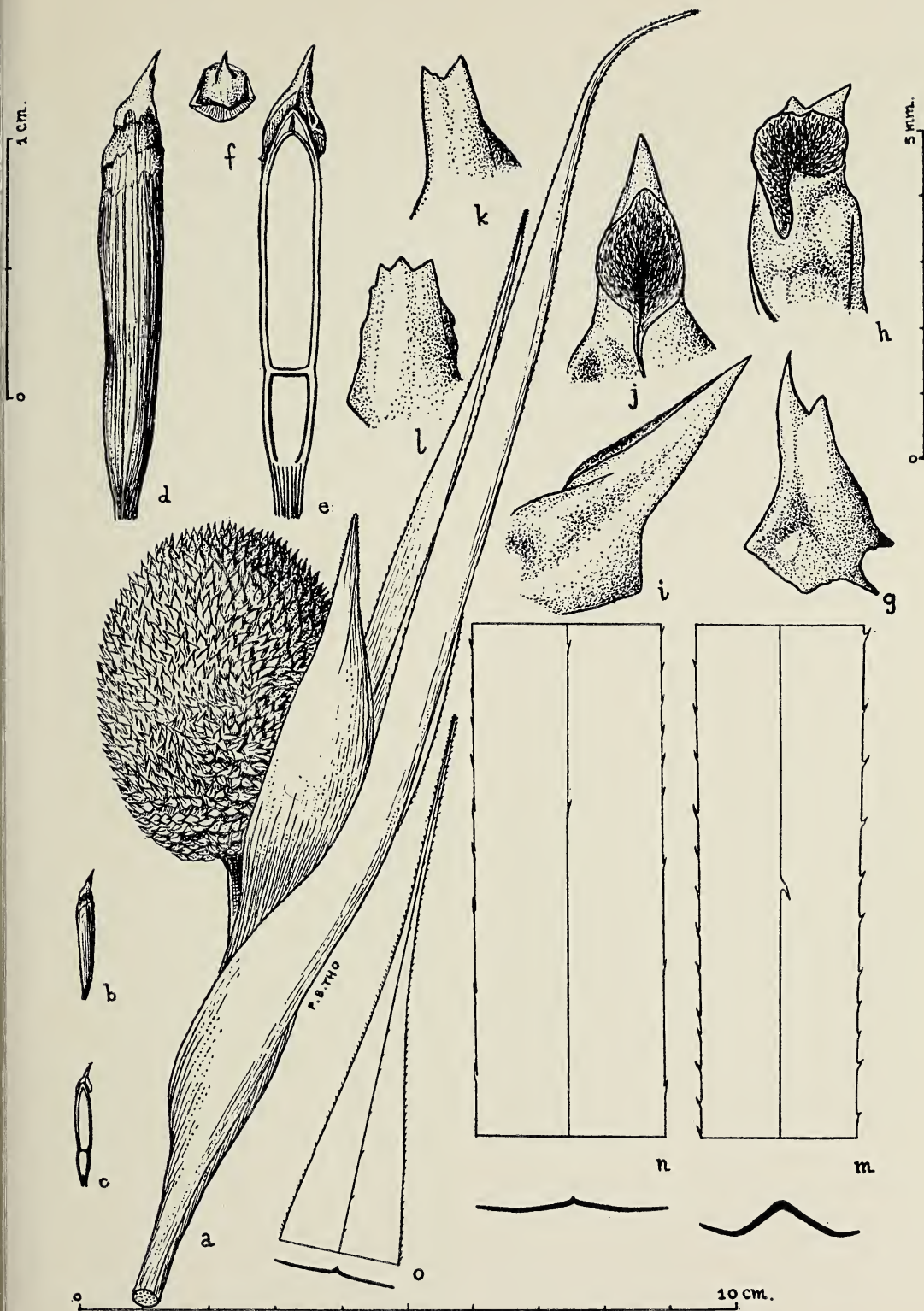


FIG. 164. *Pandanus brevicornutus* St. John, from holotype. *a*, Syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe apex and style, apical view, $\times 4$; *g*, style, distal view, $\times 10$; *h*, style and stigma, proximal view, $\times 10$; *i*, style and stigma, lateral view, $\times 10$; *j*, style and stigma, proximal view, $\times 10$; *k*, *l*, style, distal view, $\times 10$; *m*, leaf base, lower side, $\times 1$; *n*, leaf middle, lower side, $\times 1$; *o*, leaf apex, lower side, $\times 1$.

John, which has the syncarp 11–14 cm in diameter, oval-subglobose; phalanges 4.3–4.6 cm long, orange; central apical sinuses 3.5–5 mm deep; endocarp lateral walls 2–3 mm thick; and the leaves 4.8–6 cm wide, at midsection the margins with prickles 3–4 mm long, and 5–17 mm apart. *P. rubricoloratus* has the syncarp 8.5 cm in diameter, globose; phalanges 3.6 cm long, red; central apical sinuses 0.5–2 mm deep; endocarp lateral walls 1.5 mm thick; and the leaves 2.8–3 cm wide, at midsection the margins with prickles 2–2.5 mm long, and 4–12 mm apart.

The epithet is formed from the Latin words *ruber*, red; *coloratus*, colored, in reference to the red color of the fruit.

Pandanus brevicornutus sp. nov. (sect. *Rykia*)

Fig. 164

DIAGNOSIS HOLOTYPE: Frutex, ramis assurgentibus in apice 17 mm diametro luteis lucidis, foliis 41–47 cm longis 27–29 mm latis in medio sed in basi 18–22 mm latis ligulatis chartaceis proxima basem supra midnervum sulcatis alibi planis in sectione mediali cum 19–21 nervis parallelis secundariis in quoque medio nervis tertialis transversis semievidentis proxima apicem in apice 3.5 cm longo 1.5 mm lato trigono subulato semiabrupte diminuentibus, basi amplexicauli inermi sed ex 3–4 cm marginibus cum aculeis 1.5–3 mm longis 3–7 mm separatis subulatis adscendentibus obscure mahoganicoloratis lucidis, midnervo infra ex 9–10 cm cum aculeo unico 2.5 mm longo arcuato subulato reflexo, in sectione mediali marginibus cum aculeis 0.5–1.5 mm longis 6–11 mm separatis graciliter subulatis proxime adpressi-adscendentibus, midnervo infra cum aculeis 2–2.5 mm longis paucis remotis arcuatis subulatis reflexis vel adscendentibus, in apice subulato marginibus cum serrulis 0.2–0.5 mm longis 0.5–1.5 mm separatis, midnervo infra cum serrulis simulantibus 2–3 mm separatis, infructescentia cum syncarpio unico terminali erecto, pedunculo 10 cm longo 6 mm diametro cum folioso-bracteis multis, syncarpio 5.2 cm longo 4 cm diametro late ellipsoideo cum circa 960 drupis eis 16–18.5 mm longis 2–2.5 mm latis 1.5–2 mm crassis anguste cylindricis compressis 5-angulis corpore 14–15 mm longo, pileo 5–6 mm

longo basi 2 mm alta semiorbiculari, stylo 3–4 mm longo lanceolato osseoso brunneo lucido proxime curvato integro vel aliquis bifidis, stigmatem 1–1.5 mm longo elliptico vel late elliptico sulcato brunneo papilloso paene ad apicem extento, endocarpio in parte $\frac{1}{3}$ infera cartilagineo brunneo lateribus 0.1 mm crassis intra pallidis exlucidis, semine 3–4 mm longo ellipsoideo truncato, mesocarpio apicali cavernoso angusto ellipsoideo 9 mm longo, mesocarpio basali in lateribus fibroso intra carnosum 4–5 mm longo.

DESCRIPTION OF ALL SPECIMENS EXAMINED:

Shrub; branches assurgent, up to 1.3 m long, sprawling and forming a thicket, 17 mm in diameter at apex, yellowish, shining; leaves 35–50 cm long, 24–29 mm wide at the middle, 18–22 mm wide near the base, ligulate, chartaceous, yellowish green, not glaucous beneath, near the base sulcate over the midrib, elsewhere flat, at midsection with 18–21 secondary parallel nerves in each half, the tertiary cross veins barely visible only near the tip, near the tip rather abruptly tapering into a 3.5–7 cm subulate trigonous apex 1.5 mm wide, the base amplexicaul and cream-colored, unarmed, but beginning at 3–4 cm the margins with prickles 1.5–3 mm long, 3–7 mm apart, subulate, ascending, dark mahogany colored, shining; the midrib below 9–10 cm up with a prickle 2.5 mm long, arcuate subulate, reflexed; at midsection the margins with prickles 0.5–1.5 mm long, 6–11 mm apart, slender subulate, closely appressed ascending; the midrib below with a few remote prickles 2–2.5 mm long, arcuate subulate, reflexed or ascending; on the subulate apex the margins with serrulations 0.2–0.5 mm long, 0.5–1.5 mm apart; the midrib below with similar ones 2–3 mm apart; pistillate infructescence with a single, terminal, erect syncarp (rarely a smaller, lateral, secondary one, globose and 2 cm in diameter); peduncle 10–15 cm long, 4–6 mm in diameter, with numerous leafy bracts; syncarp 3.5–5.2 cm long, 3–4 cm in diameter, when young cream colored, broadly ellipsoid, bearing 600–960 drupes, these 16–18.5 mm long, 2–2.5 mm wide, 1.5–2 mm thick, narrowly cylindric, compressed, 5-angled, upper $\frac{1}{4}$ free, the body 14–15 mm long; pileus 5–6 mm long, the base 2 mm high, semiorbicular, crowned by a style 3–4 mm long, prolonged

into a lanceolate, entire or less commonly bifid beak, bony, brownish, shining, flattened, proximally curved; stigma 1–1.5 mm long, elliptic or broadly so, creased, brown, papillose, running almost to the apex; endocarp in lower $\frac{1}{3}$, cartilaginous, brown, walls 0.1 mm thick, the inner surface pale, dull; seed 3–4 mm long, ellipsoid, truncate; apical mesocarp a slender cavity 9 mm long; basal mesocarp fibrous up the sides, fleshy within, 4–5 mm long.

HOLOTYPE: Malaya, Johore, Sungei Kayu, in swamp, 17 Oct. 1936, *Kiah bin Haji Salleh* 32,102 (SING).

SPECIMENS EXAMINED: Malaya, S[ungei] Kayu, Mawai-Jemaluang Road, in swamp, evidently fruits commonly, 11 Oct. 1936, *E. J. H. Corner* 32,460 (SING), in large part, but not the loose fruit), (SING).

DISCUSSION: *P. brevicornutus* is a member of the section *Rykia*, as is its closest relative, the Malayan species *P. kedabensis* St. John, which has the syncarp 12.5 cm long, 11 cm in diameter; drupes 4.2–4.4 cm long, 8–13 mm wide, narrowly oblanceoloid; style 4–5 mm long, bifurcate, the lobes mostly divergent; endocarp with apical narrow pyramidal projection; seeds 15–16 mm long; leaves 4.5–4.6 cm wide, and at midsection with 43 secondary parallel veins in each half. *P. brevicornutus* has the syncarp 3.5–5.2 cm long, 3–4 cm in diameter; drupes 16–18.5 mm long, 2–2.5 mm wide, narrowly cylindric; style 3–4 mm long, lanceolate, less commonly unevenly bifid; endocarp apex truncate; seeds 3–4 mm long; leaves 24–29 mm wide, and at midsection with 18–21 secondary parallel veins in each half.

The new epithet is taken from the Latin words *brevis*, short; *cornutus*, horned, and is chosen in reference to the short, hornlike style of this species.

Pandanus distentus sp. nov. (sect. *Rykia*)

Fig. 165

DIAGNOSIS HOLOTYPE: Planta cum foliis 1.8–3 m longis 9 cm latis crassiter coriaceis 1-sulcatis 2-plicatis in sectione M-formatis in sectione mediali cum 61 nervis parallelis secundariis prominentibus in quoque medio nervis tertiis fortibus in dimidia ultima reticulam formantibus lamina ligulata valde contracta in

apice 29 cm longo subulato caudato trigono eo 10 cm ex apice 1 mm lato basi non conservati, proxima basem marginibus cum spinis 5–7 mm longis 11–24 mm separatis deltoideo-subulatis complanatis subarcuato-adscendentibus pallidis sed apicibus nigris, midnervo infra cum spinis teretibus 5–6 mm longis 12–30 mm distantibus subulatis arcuatis reflexis nigris basibus crassis, in sectione mediali marginibus cum spinis 4–5.5 mm longis crasse subulatis arcuatis adscendentibus saepe tota pallidis, midnervo infra cum spinis 4 mm longis 4.5–6 cm separatis crasse subulatis arcuatis complanatis valde reflexis, in sectione diminuenti marginibus cum subulato-serris 1.2–2 mm longis 1–4 mm separatis arcuatis, midnervo infra angusto salienti cum aculeis simulantibus, in apice caudato marginibus et midnervo infra cum serrulis 0.2–0.4 mm longis 1–4 mm separatis, inflorescentia foeminea "circa 30 cm longa," pedunculo 10 mm diametro trigono folioso-bracteato probabalter cum syncarpio solitario, syncarpio circa 15 cm longo et 10–11 cm diametro ellipsoideo, drupis multis 34–36 mm longis (vel stylo sequi 37–41 mm) 8–12 mm latis 7–12 mm crassis anguste oblanceoloideis subcompressis 5–7-angulosis corpore 30–32 mm longo anguste ellipsoideo vel filiformi lateribus subcurvatis vel planis, pileo 9–12 mm longo basi pyramidali-semiorbiculari laevi, stylo 3–5 mm longo osseoso rigido lucido compresso proxime curvato basi late oblonga parte supera acute bifida cum lobis subulatis sed eis cum lateribus exterioribus extensis undulatis, stigmatibus 3–4 mm longo late ovoideo bifido ad apices extenso brunneo papilloso, endocarpio submediali osseoso obscure brunneo lateribus 1 mm crassis intus lucido in apice cum projectione centrali anguste conico, semine 15 mm longo 5 mm diametro ellipsoideo obtuso, mesocarpio apicali cavernoso cum fibris et membranis, mesocarpio basali in lateribus fibroso intra carnosum.

DIAGNOSIS OF HOLOTYPE: Stature not recorded; leaves 1.8–3 m long, 9 cm broad, thick coriaceous, 1-ribbed and 1-furrowed, 2-pleated, in section M-shaped, at midsection with 61 parallel secondary veins in each half, these rather prominent except at base, the tertiary cross veins strong, transverse, forming oblong meshes, these at least from the middle outwards giving

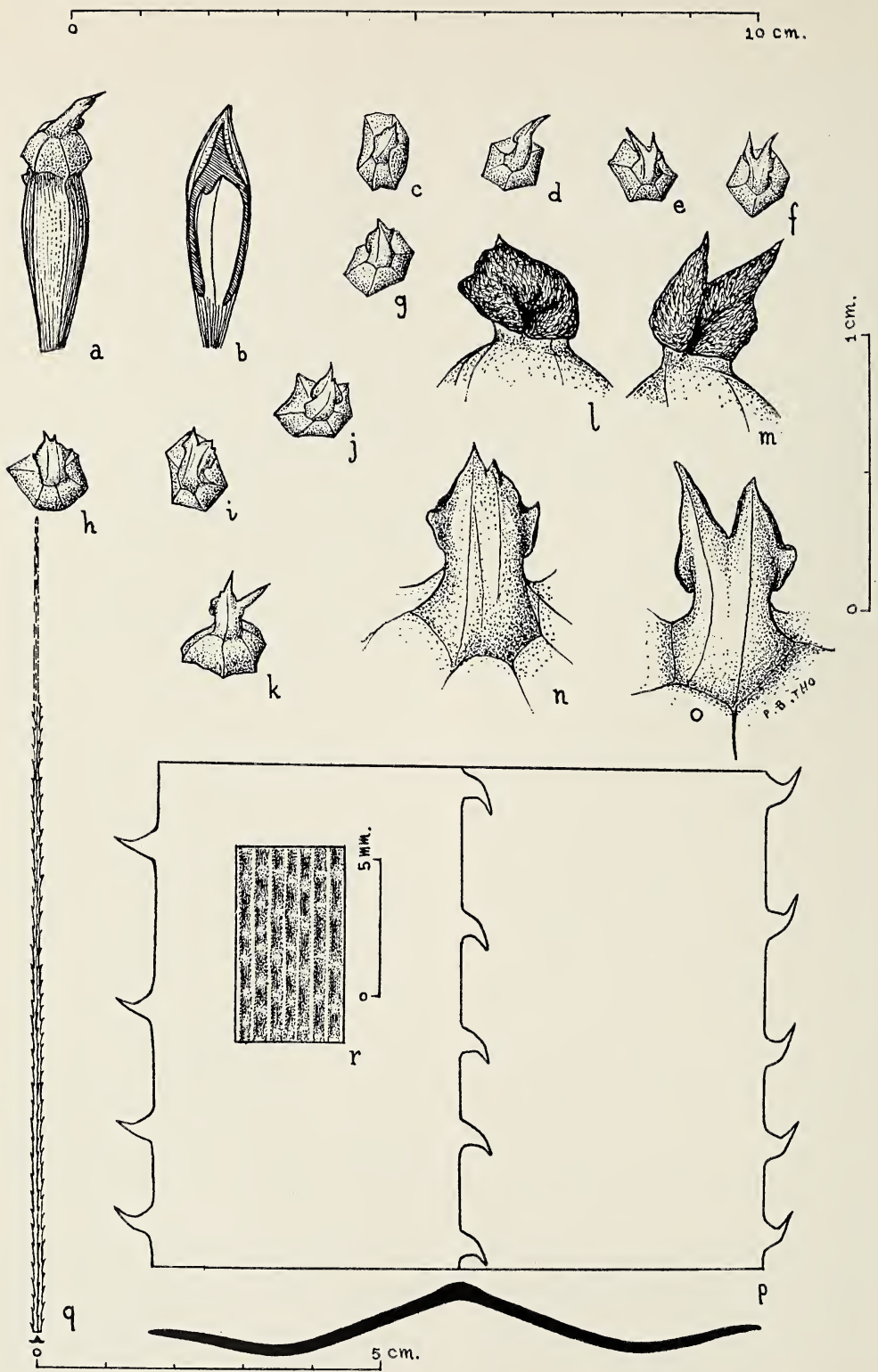


FIG. 165. *Pandanus distentus* St. John, from holotype. *a*, Phalange, lateral view, $\times 1$; *b*, phalange, longitudinal median section, $\times 1$; *c-k*, drupe and style, apical view, $\times 1$; *l, m*, stigma, proximal view, $\times 4$; *n, o*, style, distal view, $\times 4$; *p*, leaf base, lower side, $\times 1$; *q*, leaf apex, lower side, $\times 1$; *r*, leaf venation, lower side, near base, $\times 4$. (*e, f, h, i, k*, Frequent and most typical styles; *c, d, g, j*, infrequent forms of style.)

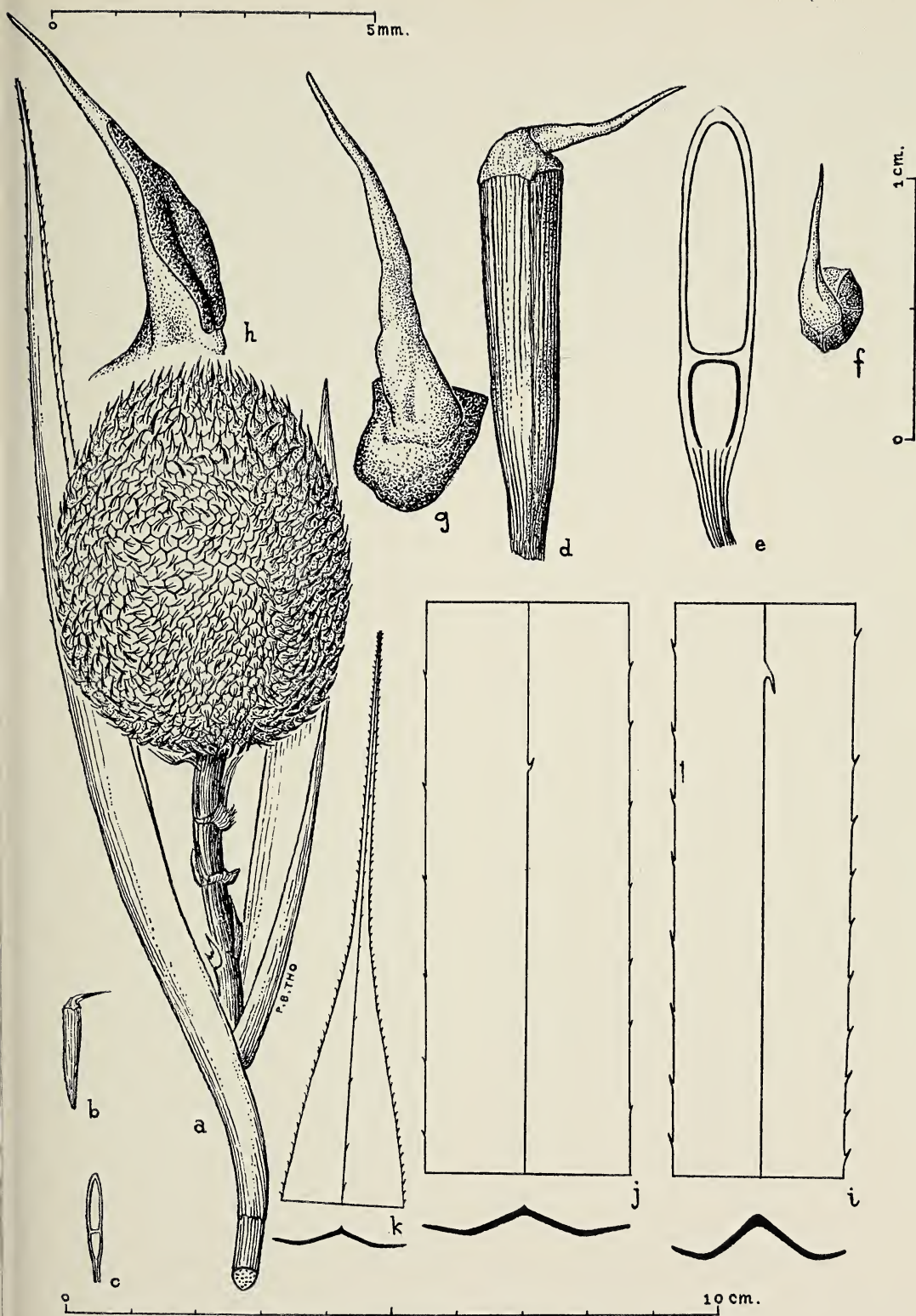


FIG. 166. *Pandanus inundatus* St. John, from holotype. *a*, Infructescence, habit, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe and style, apical view, $\times 4$; *g*, drupe apex and style, apical view, $\times 10$; *h*, style and stigma, proximal view, $\times 10$; *i*, leaf base, lower side, $\times 1$; *j*, leaf middle, lower side, $\times 1$; *k*, leaf apex, lower side, $\times 1$.

both leaf surfaces a reticulate appearance, the blade ligulate, rather sharply contracted to a 29 cm subulate, caudate, trigonous apex, this at 10 cm down from the tip 1 mm wide, the base not preserved, near the base the margins with thorns 5–7 mm long, 11–24 mm apart, deltoid, subulate, flat, slightly arcuate ascending, pale except for tiny blackish tips; the midrib below with heavy based, terete spines 5–6 mm long, 12–30 mm apart, subulate, arcuate, reflexed, black; at lower third the margins with spines 4–5.5 mm long, 13–29 mm apart, heavy subulate, arcuate, ascending, pale throughout or with minute blackish tips; the midrib with spines 4 mm long, 4.5–6 cm apart, flat, heavy subulate, arcuate, strongly reflexed; on the contracting area near the tip the margins with prickles 1.2–2 mm long, 1–4 mm apart, subulate-tipped serrae, arcuate; the midrib below narrow, sharp, salient, bearing similar prickles; on the caudate apex the margins and midrib below with serrulations 0.2–0.4 mm long, 1–4 mm apart; pistillate inflorescence "about 30 cm. long," peduncle about 10 mm in diameter, 3-sided, leafy bracted, apparently bearing a single syncarp, this apparently about 15 cm long and 10 or 11 cm in diameter, ellipsoid (an estimate based upon a part of the core, two slabs of drupes, and many separate ones); drupes numerous 34–36 mm long (or following the curve of the style 37–41 mm), 8–12 mm wide, 7–12 mm thick, narrowly oblanceoloid, a little compressed, 5–7-angled, the body 30–32 mm long, narrowly ellipsoid or fusiform, the sides gently curved or plane; pileus 9–12 mm long, the base pyramidal-semiorbicular, smooth; style 3–5 mm long, bony, rigid, shining, flattened, proximally curved, the base broad oblong, the upper part sharply bifid with subulate tips but the outer sides with broad, more or less undulate, expanded margins; stigma 3–4 mm long, broad ovoid, bifid, running to the apices, brown, papillose; endocarp submedian, bony, dark brown, the lateral walls 1 mm thick, the inner surface shining, with a narrow conical projection running upward into the beak; seed 15 mm long, 5 mm in diameter, ellipsoid, obtuse; apical mesocarp cavernous, but with fibers and membranes; basal mesocarp fibrous up the margins, fleshy within.

HOLOTYPE: Malaya, Pulau Penang, Telok Aling, native, common, 23 Oct. 1951, *J. Sinclair* 39,382 (SING).

DISCUSSION: *P. distentus* is a member of the section *Rykia*, as is its closest relative, the Malayan species *P. longicaudatus* Holtum & St. John, a species with the drupes 41–44 mm long, the lateral ones with styles 4–8 mm long, bifurcate, the forks subulate; endocarp walls 1.5–2 mm thick; leaves 4.7–6 cm wide, the caudate apex 15–22 cm long, secondary nerves 48 in each half, and near the base the margins with thorns 3–5 mm long, 6–14 mm apart. *P. distentus* has the drupes 37–41 mm long, the styles sharply bifid, but the lobes with undulate, expanded outer margins; endocarp walls 1 mm thick; leaves 9 cm wide, the caudate apex 29 cm long, the secondary nerves 61 in each half, and near the base the margins with thorns 5–7 mm long, 11–24 mm apart.

The new epithet is the Latin participle *distentus*, distended, and is given in reference to the lateral extensions of the style forks.

Pandanus inundatus sp. nov. (sect. *Rykia*)

Fig. 166

DIAGNOSIS HOLOTYPE: Frutex, caule in apice 8 mm diametro, foliis 37–42 cm longis 30–32 mm latis in medio sed proxima basem 20 mm latis chartaceis et sulcatis minime 2-plicatis ligulatis ad apicem diminuentibus in apice trigono subulato 4 cm longo 1–1.5 mm lato, in sectione mediali cum 19–20 nervis parallelis secundariis conspicuis in quoque dimidio, nervis tertialis nullis, basi amplexicauli et inermi sed ex 3–3.5 cm marginibus cum aculeis 2.5–3.5 mm longis 4–8 mm separatis subulatis arcuatis brunneis, midnervo infra ex 10 cm cum aculeis simulantibus 3 mm longis reflexis remotis paucis, in sectione mediali marginibus cum aculeis 0.8–1 mm longis 7–20 mm separatis subulatis adpresse adscendentibus, midnervo infra cum aculeo unico vel pluribus remotis 1.5 mm longis compressis arcuatis adscendentibus, in apice subulato marginibus et midnervo infra cum aculeis 0.3–0.5 mm longis 0.5–1.5 mm separatis subulatis adscendentibus, infructescentia terminali cum capite unico, pedunculo 12 cm longo 4 mm diametro trigono folioso-bracteato, syncarpio 6 cm longo 4.5 cm diametro ellipsoideo sed minime

3-planato cum circa 832 drupis eis 17–19 mm longis 2–2.5 mm latis 1.5–2 mm crassis viridibus corpore 14–15 mm longo anguste cylindrico compresso 5–6-anguloso, pileo 6–8 mm longo basi 2–2.5 mm alta ellipsoidea laevi, stylo 5–6 mm longo plerumque proximo frequente subreflexo, stigmate 2–3.5 mm longo anguste elliptico brunneo papilloso ex apice distante, endocarpio in parte $\frac{1}{3}$ infera cartilagineo pallide brunneo lateribus 0.1 mm crasso intra exclucido, semine 2.7 mm longo ellipsoideo, mesocarpio apicali cavernoso 8 mm longo, mesocarpio basali in lateribus fibroso intra carnosio.

DESCRIPTION OF ALL SPECIMENS EXAMINED:

Shrub up to 1.7 m tall, 8–15 mm in diameter, often decumbent; bark dark mahogany-colored, shining; internodes 7–11 mm long; prop roots several and as much as 40 cm long, 7–8 mm in diameter, brown, with loose spirals of adventitious rootlets 2–5 mm long, divergent, prickly-like; leaves 37–65 cm long, 25–34 mm wide at the middle, 20–24 mm wide near the base, chartaceous, above glossy dark green, below yellowish green, at base channeled above the midrib, slightly 2-pleated, ligulate, the apex narrowed to a 4–5 cm trigonous subulate tip 1–1.5 mm wide, at midsection with 18–22 secondary parallel conspicuous veins in each half, but no clearly visible tertiary veins, the base amplexicaul, unarmed, but beginning at 3–3.5 cm the margins with prickles 2.5–3.5 mm long, 4–8 mm apart, subulate, bent upwards, brownish; the midrib below beginning at 10 cm with a few remote similar prickles 3 mm long, reflexed; at midsection the margins with prickles 0.8–1 mm long, 7–20 mm apart, subulate, appressed ascending; the midrib below with one or several remote prickles 1.5 mm long, compressed, heavy based, arcuate ascending; on the subulate tip the margins and midrib beneath with prickles 0.3–0.5 mm long, 0.5–1.5 mm apart, subulate, ascending; infructescence terminal, with a single head, or rarely two heads; peduncle 10–17 cm long, 4–6 mm in diameter, trigonous, leafy bracted, sometimes pendent; syncarp 4–6 cm long, 3–4.5 cm in diameter, ellipsoid but slightly 3-sided, bearing 832–1,040 drupes, these 17–19 mm long, 2–2.5 mm wide, 1.5–2 mm thick, green, the body 14–15 mm long, narrowly cylindric, compressed, 5–6-angled; pileus 6–8 mm

long, the base 2–2.5 mm high, ellipsoid, smooth; style 5–6 mm long, mostly proximal in attachment, often somewhat reflexed; stigma 2–3.5 mm long, narrowly elliptic, brown, papillose, remote from the apex; endocarp in lower $\frac{1}{3}$, cartilaginous, pale brown, the walls 0.1 mm thick, the inner surface dull; seed 2.7 mm long, ellipsoid; apical mesocarp a cavern 8 mm long; basal mesocarp fibrous up the sides, fleshy within.

HOLOTYPE: Malaya, Johore, Sungei Sedili, 30 July 1939, *Kiah bin Haji Salleh* 63,926 (SING).

SPECIMENS EXAMINED: Malaya, Johore, 5½ miles, Kota Tinggi-Mawai Road, in very swampy places in backwaters of streams, forming more or less pure stands, 13 April 1935, *E. J. H. Corner* 29,237 (BO, SING); Johore S[ungei] Berassau, Mawai-Jemaluang Road, frequent in swampy forest, 6 Feb. 1935, *E. J. H. Corner* 28,744 (SING); ditto, flopping, gregarious in wet hollows in swampy forest, 7 Feb. 1935, *Corner* s. n. (SING); ditto, gregarious in standing water, low elevation, 28 April 1935, *Corner* 29,361 (BO, SING); ditto, in standing swamp by the stream, 5 Jan. 1936, *Corner* 29,997 (SING).

DISCUSSION: *P. inundatus* is a member of the section *Rykia* and in that section is its closest relative, *P. Scortechinii* Martelli, a species with drupes 12–13 mm long; style terminal, 4–5 mm long; stigma linear; endocarp slightly submedian; seed 6 mm long; leaves 25–27 cm long, near the base 14 mm wide, at midsection the secondary nerves 15–16 in each half, tertiary cross veins visible in the outer half, at midsection the margins with weak prickles 0.2–0.3 mm long, flat appressed, close or remote or none. *P. inundatus* has the drupes 17–19 mm long; style of lateral drupes markedly lateral, 5–6 mm long; stigma narrowly elliptic; endocarp in lower $\frac{1}{3}$; seed 2.7 mm long; leaves 37–65 cm long, near the base 20 mm wide, at midsection the secondary nerves 18–22 in each half, no clearly visible cross veins; at midsection the margin with prickles 0.8–1 mm long, 7–20 mm apart, subulate, appressed ascending.

This was probably the species illustrated by Martelli (*Webbia* 4(2): t. 32, f. 1–3a, 1914) as his *P. johorensis* Martelli. Martelli did not have the habit of indicating the specimen from

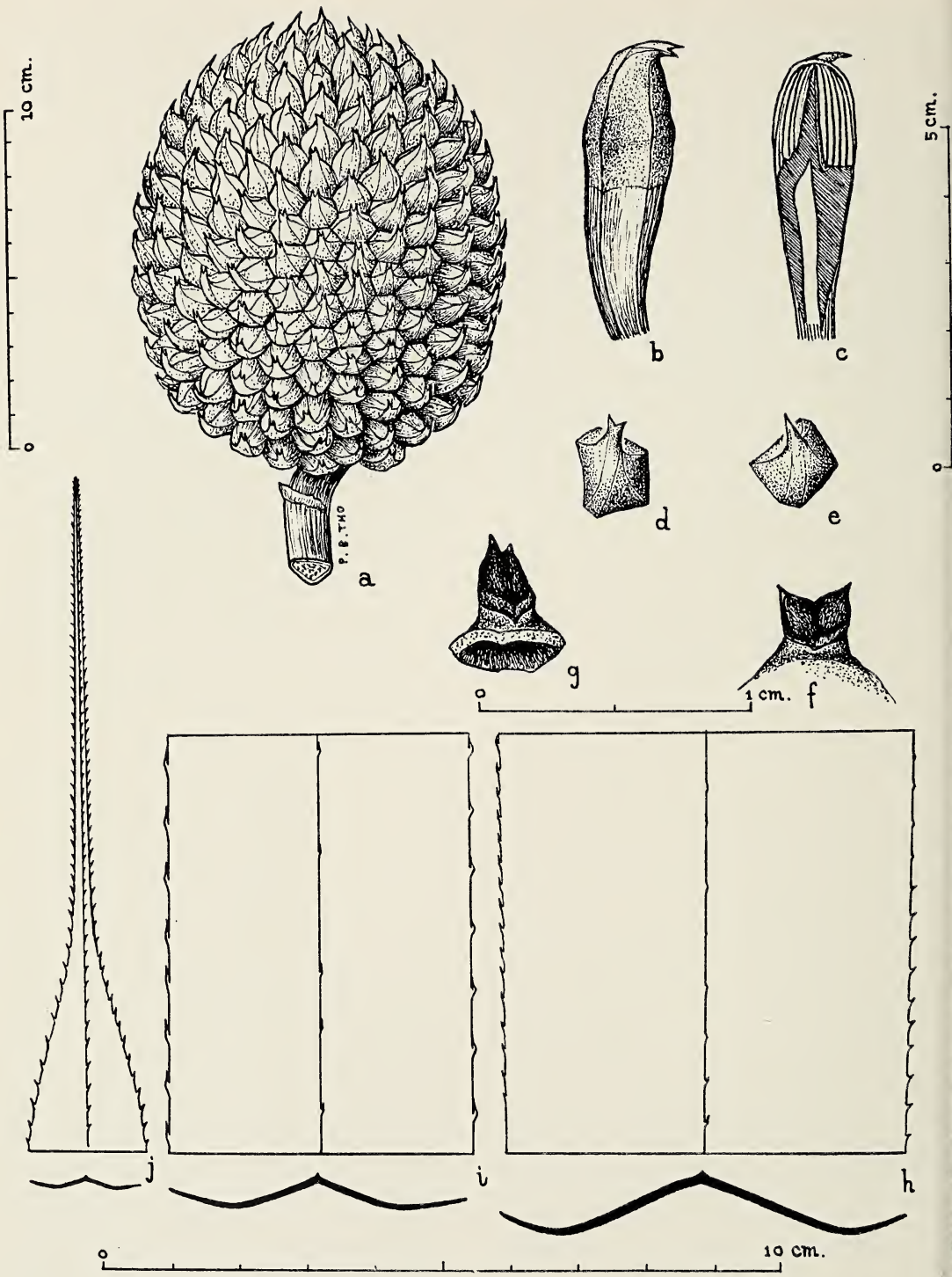


FIG. 167. *Pandanus kedabensis* St. John, from holotype. *a*, Syncarp, $\times \frac{1}{2}$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, lateral drupe and style, apical view, $\times 1$; *e*, apical drupe and style, apical view, $\times 1$; *f*, *g*, stigma, proximal view, $\times 4$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$.

which he made his illustrations. Evidence is now accumulating to show that he did not consistently illustrate the types, but rather that he used the best specimen at hand when making the drawing. Having seen and illustrated the type number of *P. johorensis*, it is evident to the writer that Martelli's figures on his plate 32, published 10 years after he published the species, were drawn from another specimen, not the holotype. This other specimen seems to be like those here described as the new species *P. inundatus*.

The new epithet is the Latin participle *inundatus*, flooded, given in reference to the habitat of the species.

Pandanus kedahensis sp. nov. (sect. *Rykia*)

Fig. 167

DIAGNOSIS HOLOTYPE: Planta cum "foliis grandibus," pedunculo 22 cm vel plus longo 12 mm diametro trigono folioso-bracteato, bracteis 47–70 cm longis 4.5–4.6 cm latis coriaceis 1-costatis 2-plicatis in sectione mediali cum 43 nervis parallelis secundariis in quoque latere eis supra evidentibus et infra prominentibus, nervis tertialis prominentibus et reticulum cum sectionibus oblongis formantibus lamina ligulata ad basem spathacea sed ex 14 cm marginibus et midnervo infra cum aculeis 0.5–1 mm longis 1–4 mm separatis subulatis adscendentibus apicibus brunneis, in sectione mediali marginibus cum aculeis 2–3 mm longis 2–10 mm separatis arcuatis subulatis adscendentibus adpressis semisombratis in margine undulato, midnervo infra angusto salienti cum aculeis 1 mm longis 1–4 cm separatis arcuatis subulatis adscendentibus, in apice caudato marginibus et midnervo infra cum subulato-serrulis 0.5–0.8 mm longis 1–2 mm separatis, syncarpio 12.5 cm longo 11 cm diametro late ovoideo cum circa 544 drupis eis 4.2–4.4 cm longis 8–13 mm latis 7–12 mm crassis anguste oblanceoloideis 5–6-angulatis parte $\frac{2}{5}$ supera libera corpore 3.8–4 cm longo, pileo 13–14 mm longo pyramidal-ovoideo 5–6-angulato laevi plerumque ex apice styli planato proxime inclinato truncato, stylo 4–5 mm longo oblongo osseoso brunneo lucido bifurcato lobis plerumque divergentibus, stigmatibus 2–3 mm longo proximo late ovato bifido brunneo papilloso paene in apicibus extento, endocarpio in

parte $\frac{2}{5}$ infera obscure brunneo osseoso cum projectione angusto pyramidal- apicali lateribus 2–3 mm crassis intra rugosis lucidisque, semine 15–16 mm longo 2 mm diametro, mesocarpio apicali cavernoso et cum membranis albis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Stature not recorded; "large leaved"; peduncle more than 22 cm long, 12 mm in diameter, 3-sided, leafy bracted, these bracteal leaves 47–70 cm long, 4.5–4.6 cm wide, coriaceous, 1-ribbed, 2-pleated, at midsection with 43 parallel secondary nerves in each half, these visible above, prominent below, the tertiary cross veins conspicuous, at right angles, forming meshes mostly oblong, the blade ligulate, towards the base spathaceous enlarged; at 14 cm above the base the margins and midrib below with prickles 0.5–1 mm long, 1–4 mm apart, subulate, ascending, brown-tipped; at midsection the margins undulate and with partly countersunk prickles 2–3 mm long, 2–10 mm apart, arcuate subulate, flat appressed, ascending, brown-tipped; midrib below narrow, salient, with prickles 1 mm long, 1–4 cm apart, arcuate subulate, ascending; the caudate apex having the margins and midrib below with subulate tipped serrulations 0.5–0.8 mm long, 1–2 mm apart; syncarp 12.5 cm long, 11 cm in diameter, broadly ovoid, bearing about 544 drupes, these 4.2–4.4 cm long, 8–13 mm wide, 7–12 mm thick, narrowly oblanceoloid, 5–6-angled, upper $\frac{2}{5}$ free, the body 3.8–4 cm long; pileus 13–14 mm long, pyramidal-ovoid, 5–6-angled, smooth, mostly truncate by the flattened upper side of the sharply proximally bent style, this 4–5 mm long, oblong, bony, brown, shining, bifurcate, the lobes mostly diverging; stigma 2–3 mm long, proximal, broad ovate, bifid, brown, papillose, extending almost to the apices; endocarp in lower $\frac{2}{5}$, dark brown, bony, with a narrow pyramidal apical extension, the lateral walls 2–3 mm thick, in inner surface rugose, shining; seed 15–16 mm long, 2 mm in diameter; apical mesocarp one large cavern with white membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Malaya, Kedah, Kedah Peak, in low forest, not far from summit, 3,500 ft. alt., 1 April 1925, R. E. Holttum 14,858 (SING).

DISCUSSION: *P. kedahensis* is a member of the section *Rykia*, as is its closest relative, the

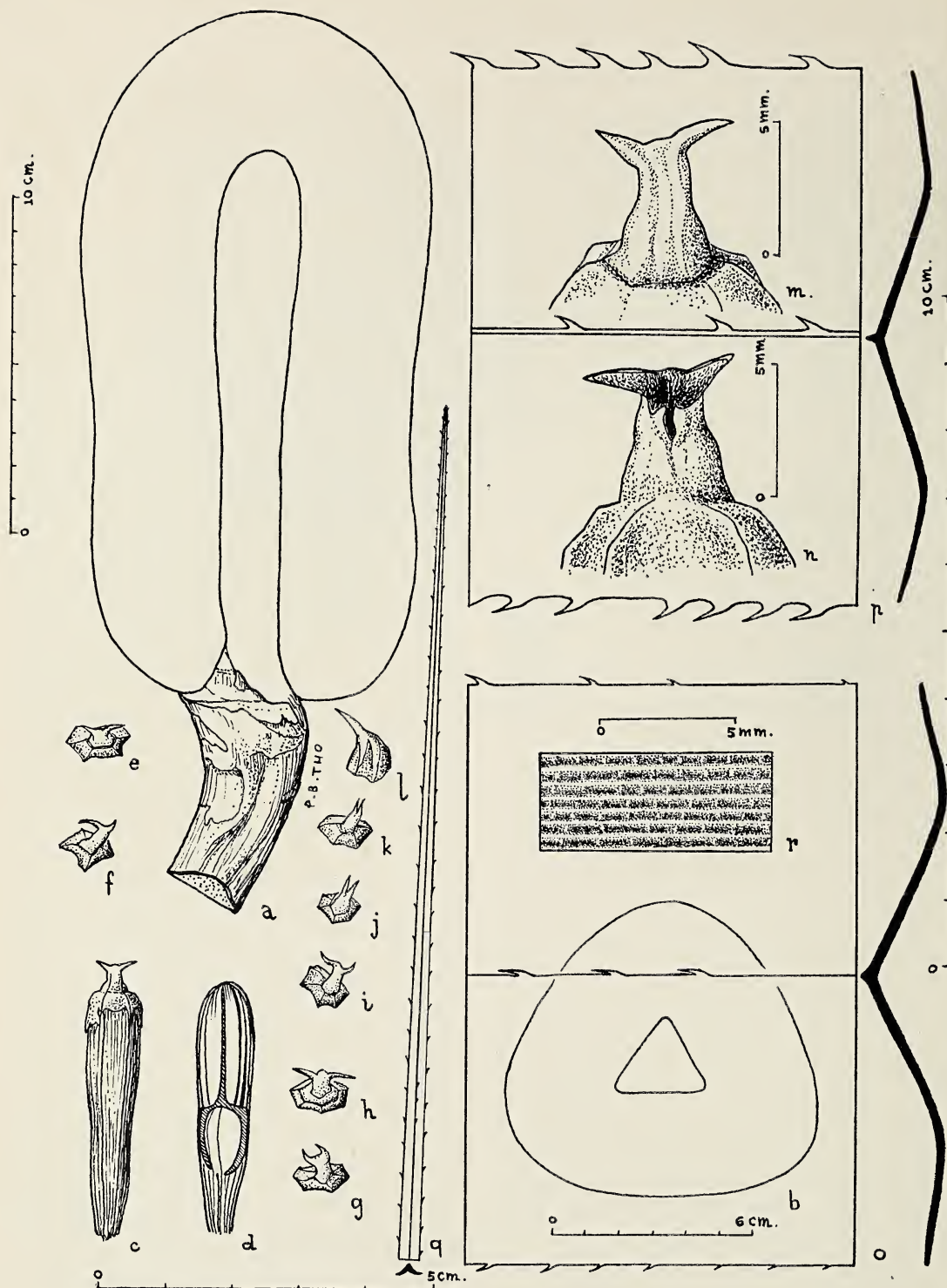


FIG. 168. *Pandanus serratus* St. John, from holotype. *a*, Syncarp profile, $\times \frac{1}{2}$; *b*, syncarp, outline of transverse section, $\times \frac{1}{2}$; *c*, drupe, distal view, $\times 1$; *d*, drupe, longitudinal median section, $\times 1$; *e-k*, lateral drupes and styles, apical view, $\times 1$; *l*, apical drupe, apical view, $\times 1$; *m*, carpel apex and style, distal view, $\times 4$; *n*, carpel apex, proximal view, $\times 4$; *o*, leaf base, lower side, $\times 1$; *p*, leaf middle, lower side, $\times 1$; *q*, leaf apex, lower side, $\times 1$; *r*, venation near leaf base, lower side, $\times 4$.



FIG. 169. *Pandanus albibracteatus* St. John, from holotype and paratype. *a*, Clump of pistillate holotypic trees at top of beach, with figure of Cheang Kok Choy; *b*, branch with syncarp; *c*, foliage of paratype, *St. John* 26,370; *d*, staminate paratype, *St. John* 26,370, with figure of Cheang Kok Choy.

Malayan species *P. longicaudatus* Holtum & St. John, a species with the peduncle 22 mm in diameter; syncarp 16–17 cm long, with about 900 drupes; pileus pyramidal-hemispheric; stigma 3–3.5 mm long; endocarp walls 1.5–2 mm thick, the inner surface smooth; and the seed 6 mm in diameter. *P. kedahensis* has the peduncle 12 mm in diameter; syncarp 12.5 cm long, with about 544 drupes; pileus pyramidal-ovoid; stigma 2–3 mm long; endocarp walls 2–3 mm thick, the inner surface rugose; and the seed 2 mm in diameter.

The new epithet is a Latinization of the name of the type locality.

Pandanus serratus sp. nov. (sect. *Rykia*)

Fig. 168

NOM. VERN.: "mengkuang ayer."

DIAGNOSIS HOLOTYPI: Licet aquatica in aqua vadosa, foliis 1.5 m longis in media 8.5 cm latis ad terminos ambos diminuentibus crassiter coriaceis supra viridibus infra minime pallidioribus 1-sulcatis 2-plicatis in sectione depresso M-formatis in sectione mediali cum 75 nervis parallelis secundariis in quaque dimidia in apice longe subulato diminuentibus basi amplexicauli inermi sed ex 20 cm marginibus cum aculeis 1–2 mm longis 5–10 mm distantibus valde

arcuato-subulatis pallidis adscendentibus, midnervo infra inermi, in sectione mediali marginibus cum spinis 6.5–7 mm longis 7–16 mm separatis fortiter arcuato-subulatis adscendentibus basi incrassata 4–5 mm lata apicibus rubris,

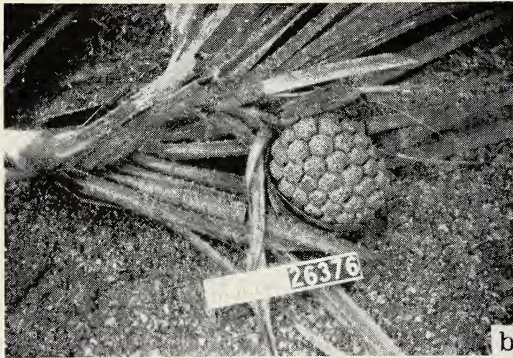


FIG. 170. *a*, Staminate inflorescence and leaf of *Pandanus albibracteatus*, paratypic specimen, St. John 26,370; *b*, *Pandanus ambiglaucus* St. John, holotype, branch, foliage, and syncarp; *c*, *Pandanus inclinatus* St. John, holotype, branch, foliage, and syncarp.

midnervo angusto salienti infra cum serris 2–2.5 mm longis 10–15 mm separatis adpresse adscendente subulatis, proxima apicem marginibus cum serrulis 0.5–1 mm longis 4–8 mm separatis, midnervo infra cum serrulis minutis remotis paucis; inflorescentia foeminea erecta cum 1 syncarpio, pedunculo 14 cm longo 1 cm diametro trigono bracteato, syncarpio 20.5 cm longo et proxima apicem 11 cm diametro, in media 9.5 cm diametro et basi subcylindrica, syncarpio 3-laterato apice obtuso cum circa 4,300 drupis eis 28–37 mm longis eis medialis basalisque 5–8 mm latis 4–6 mm crassis sed illis superis 9–12 mm latis 7–9 mm crassis oblanceoloideis, corpore 23–32 mm longo 5–6-angulato, pileo 4–8 mm longo basi semiorbiculari-pyramidali laevi, stylo 3–5 mm longo osseoso brunneo lucido eis lateralibus et inferioribus 2.5–4 mm latis oblongis in basi latioribus gradatim proxime curvatis apice bifurcato lobis 1–3 mm longis plerumque divergentibus eis terminalibus cum stylo corniformi integro, stigmatibus 3–4 mm longis lanceolatis in lobis sed infra connatis brunneis papillosis proximis olim ad apices continuentibus, endocarpio in parte $\frac{1}{3}$ infera osseoso obscure mahogani-colorato lateribus 1 mm crassis pagina interiori lucida apice cum extensioni subulato centrali, semine 1 cm longo anguste obovoideo, mesocarpio apicali cavernoso 17 mm longo fibris marginalibus multis centralibus paucis et cum medulla, mesocarpio basali fibroso et carnosio.

DIAGNOSIS OF HOLOTYPE: Apparently aquatic, rooting in shallow fresh water; leaves about 1.5 m long, at the middle 8.5 cm wide, tapering towards both ends, thick coriaceous, green above, slightly paler below, 1-ribbed, 2-pleated, in section low M-shaped, at midsection with 75 secondary parallel veins in each half, tapering towards the tip into a long subulate apex, but the actual tip not preserved, the base amplexicaul and unarmed, but the margins beginning at 20 cm up with prickles 1–2 mm long, 5–10 mm apart, stout arcuate subulate, pale, ascending; the nearby midrib below unarmed; at midsection the margins with spines 6.5–7 mm long, 7–16 mm apart, heavy, arcuate subulate, ascending, the base much thickened, 4–5 mm wide, the tips reddish; the midrib below with appressed ascending subulate tipped serrae 2–2.5

mm long, 10–15 mm apart, on the narrow salient midrib; near the apex the margins with serrulations 0.5–1 mm long, 4–8 mm apart; the midrib below with a few, tiny, very remote serrulations; pistillate inflorescence erect, bearing

1 syncarp; peduncle 14 cm long, 1 cm in diameter, 3-sided, bracteate; syncarp 20.5 cm long, 11 cm in diameter near the tip, 9.5 cm at the middle, and near the base subcylindric, 3-sided, the apex obtuse, bearing about 4,300 drupes,



FIG. 171. *Pandanus incrassatus* St. John, holotype, *St. John* 26,374. *a*, Habit, foliage, and syncarp, with figure (right) of Paul Weissich; *b*, trunk; *c*, trunk and prop roots; *d*, branch, foliage, and syncarp.

these 28–37 mm long, the middle and lower ones 5–8 mm wide, 4–6 mm thick; the upper and apical ones 9–12 mm wide, 7–9 mm thick, oblanceoloid; the body 23–32 mm long, 5–6 angled; pileus 4–8 mm long, the base semi-orbicular-pyramidal, smooth; style 3–5 mm long, bony, brown, shining, of the lateral and lower ones 2.5–4 mm wide, oblong, broadening at base, gently proximally curved and at apex bifurcate, the lobes 1–3 mm long, mostly divergent, but the terminal drupes with simple, horn-like style; stigmas 3–4 mm long, lanceolate on the lobes but united below, brown, papillose, proximal, running almost to the point of the style; endocarp centering in lower $\frac{1}{3}$, bony, dark mahogany-colored, the walls 1 mm thick, the inner surface shining, the apex with a central, subulate prolongation; seed 1 cm long, narrowly obovoid; apical mesocarp a cavern 17 mm long, with fibers up the margin and a few within, and with traces of a medullary pith; basal mesocarp fibrous and fleshy.

HOLOTYPE: Malaya, Pahang, S[ungei] Bera,

w. Tasek Bera, low elevation, 15 Oct. 1930, M. R. Henderson 24,137 (SING).

DISCUSSION: *P. serratus* is a member of the section *Rykia*, as is its closest relative, *P. heterostigma* (Martelli) Martelli, a Sumatran species that has a raceme with 7–10 heads; syncarps 12–15 cm long, 9–19 cm in diameter; drupes 25 mm long, 7–8 mm wide; style spiniform, subulate, or narrowly oblong and bifurcate; and the leaves 2 m or more in length, 10 cm wide. *P. serratus* has the syncarp solitary, 20.5 cm long, 11 cm in diameter; drupes 28–37 mm long, 5–12 mm wide; style normally oblong, bifurcate but the apical ones stout, hornlike; and the leaves about 1.5 m long, 8.5 cm wide.

As is the case with many members of the section *Microstigma*, this species has the drupes near the apex of the syncarp markedly longer and wider than those of the lower parts of the syncarp.

The new epithet is the Latin adjective *serratus*, saw-toothed, given in reference to the leaf margins.

Species Structure of the Gobiid Fish *Gillichthys mirabilis* from Coastal Sloughs of the Eastern Pacific¹

GEORGE W. BARLOW²

A RECENT ISSUE of *Systematic Zoology* (1960, vol. 9, nos. 3, 4) was devoted entirely to a symposium entitled "The Biogeography of Baja California and Adjacent Seas." One recurring theme was the affinity between forms occurring on the Pacific Coast in the Californian province (Hubbs, 1960: 134), and those in the northern part of the Gulf of California. Between these areas, in the main part of the Gulf, the fauna was said to differ, being primarily Panamic in origin (Garth, 1960; Hubbs, 1960; Walker, 1960).

The outer-coast species found in the upper Gulf of California are Pleistocene relicts, now trapped in a cul-de-sac of warm, tropical water (Hubbs, 1948: 463; 1960: 137). According to Walker (1960: 130), most of the northern species found there differ from their cognates on the Pacific Coast. As the symposium revealed, however, there has been no extensive study comparing populations of one species on the Pacific Coast with those of the same species in the Gulf of California.

The immediate objective of this investigation, although it was initiated before the symposium was conceived, was to establish the nature of the variation between populations of *Gillichthys mirabilis* Cooper. The goal was to ascertain the degree of differentiation of the form from the upper Gulf in relation to the over-all structure of the species. A brief study (Barlow, 1961a) of *G. seta* (Ginsburg) has served as comparative material to gauge the differences observed in *G. mirabilis*. *G. seta* is a close but distinct species restricted to an ex-

treme rocky habitat found only in the upper Gulf.

G. mirabilis has been cited as one example of a species from the Pacific Coast which is also found in the upper reaches of the Gulf of California (Fig. 1). It occurs in the central region of the Gulf as well. There is a break in its distribution around Cabo San Lucas, however, separating the species into a Gulf group and a Pacific Coast group (details in Barlow, 1961a).

At the inception of the present investigation *G. mirabilis* from the northern part of the Gulf of California was considered by some ichthyologists to be a distinct species, *G. detrusus* Gilbert and Scofield. Differences of opinion existed (Barlow, 1961a), and the issue was clouded by comparisons with a third species, the then undescribed *Gillichthys seta*. As will be seen, the evidence supports the conclusion of Starks and Morris (1907: 227) that *detrusus* should be regarded as a synonym of *mirabilis*.

In 1930 *G. mirabilis* from the San Diego area in southern California was introduced into the Salton Sea. The fish has become well established in that odd saline lake in the Colorado Desert of California. This has proved to be a fortunate experiment.

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ECOLOGY AND NATURAL HISTORY

The typical habitat of *mirabilis* is the intertidal coastal slough with its extensive mud flats. Less often it is a swampy lagoon, or slough, at the mouth of a dry river which most of the time is closed off from the ocean by a sand bar.

Salinity

The water in these habitats is of moderate to high salinity, hypersaline conditions being common. The maximum salinity where *mirabilis* has been recorded was 82.5 ‰ at "El Marino," north of San Felipe in the upper Gulf of California (Lars Carpelan, personal communication). The fish usually are absent where the water is fresh or only slightly brackish. Those kept in fresh-water aquaria were listless and died within 1–2 weeks, but this may have been due to the quality of the tap water. The activation time of the spermatozoa is quickest in water having a salinity of 35 ‰ (Weisel, 1948: 47).

Temperature

Aside from illumination, temperature is the one parameter of the environment to which it is related that changes more or less regularly with the latitude of the habitat. Local conditions, of course, may distort this temperature gradient. Furthermore, the Gulf of California has a climate different from that of the Pacific Coast. For these reasons, and in order to point out the extreme situation found at the Salton Sea, the meager temperature data available have been assembled and are presented in Table 1.

Air temperatures have been used instead of sea surface temperatures. In the backwaters and ponds where *mirabilis* occurs, the surface water temperatures tend to be correlated with air temperatures (Carpelan, 1957: 376; Barlow, 1958:

582), even when moderate tidal exchange takes place (personal observations).

Throughout the year on the Pacific Coast, air temperatures increase from north to south. The increase is more pronounced in summer than in winter. For example, San Diego is warmer than San Francisco by about 4–5 °C during the summer, but is only 2–3 °C warmer in the winter.

The protected Alviso ponds of southern San Francisco Bay, with their increased insolation, exhibit a special climatological situation (Carpelan, 1957: 376) that removes them from the normal gradient of temperature change associated with latitude. Air temperatures at the ponds during 1 year averaged almost 7 degrees higher than the long-range monthly means for San Francisco shown in Table 1. The climate at Alviso ponds evidently is warmer than at many truly coastal sloughs much further south.

In the Gulf of California region air temperatures increase from north to south during much of the year. But during the late, hot, summer season the situation is reversed and the mean air temperatures decrease, though only slightly, from north to south. However, the mean sea surface temperatures for August (Roden and Groves, 1959: 14) show no latitudinal trend whatsoever. Chiefly because of the reversal in the gradient of the air temperatures, the annual range of means is low in the south but is progressively greater to the north in the Gulf.

In the tidal sloughs of the Gulf of California where *mirabilis* normally is found, the summer increase from south to north in the range of water temperatures probably is augmented by the nature of the tidal change. The tidal range increases dramatically from south to north up the Gulf, reaching a maximum of 10 m at the head of the Gulf (Roden and Groves, 1959: 28). The sills of the sloughs usually are high. Thus as one proceeds north in the Gulf, the sloughs daily have a progressively longer pond phase. This means that the buffering effect of the tidal exchange will be less, and as a result the water temperatures in the sloughs will register still greater fluctuations.

The winter mean air temperatures at San Diego on the Pacific Coast, the central and northern Gulf of California areas, and the Salton

TABLE 1
MONTHLY MEAN AIR TEMPERATURES

MONTH	PACIFIC COAST ¹		SALTON SEA ²	GULF OF CALIFORNIA ³				
	San Francisco 37° 48'N	San Diego 32° 34'N	33° 18'N	West Coast		East Coast		
				Mulege 26° 53'N	La Paz 24° 10'N	Guaymas 27° 55'N	Topolo- bampo 25° 36'N	Mazatlan 23° 11'N
January	9.3	12.5	12.0	14.0	18.2	17.7	18.6	19.3
February	11.6	13.5	13.0	16.0	19.2	18.9	19.7	19.4
March	12.9	14.4	17.5	17.8	21.3	20.7	20.1	19.7
April	13.4	15.2	20.5	20.1	23.2	22.8	22.2	21.3
May	14.1	16.9	24.5	22.9	25.5	25.5	25.0	23.8
June	14.9	17.8	28.0	27.2	27.2	29.1	29.1	26.4
July	14.8	19.9	30.5	30.5	30.0	29.8	29.8	27.5
August	15.1	20.3	31.5	30.4	30.3	30.5	29.7	27.6
September	16.7	19.4	29.5	29.0	29.0	30.2	29.7	27.5
October	15.7	17.8	24.5	24.6	27.0	27.3	27.8	26.7
November	14.0	15.9	18.5	19.5	23.2	22.6	24.0	23.5
December	10.4	13.6	13.0	14.9	20.0	18.6	19.7	20.6
Range	7.4	7.8	19.0	16.5	12.1	12.8	11.2	8.3

¹ Hubbs, 1948.
² Carpelan, 1958.
³ Roden, 1958.

Sea are surprisingly similar. The summer temperatures, in marked contrast, diverge greatly. San Diego and San Francisco remain moderate, but the mean air temperatures exceed 30 C in the Gulf and Salton Sea areas.

The climate of the Salton Sea resembles that of the northern part of the Gulf of California. Both lie in the same climatological region, but the Salton Sea is a relatively small and shallow body of water surrounded by desert (Carpelan, 1958). Consequently, its climate is even more extreme than that of the upper Gulf.

Dispersal

Pelagic larvae constitute the most likely avenues of genetic exchange between disjunct populations of *mirabilis*. The adults are closely restricted to their specialized and discontinuous habitats. At least some of the larvae must be swept out to sea where they could be distributed to other bays by the oceanic currents.

There is some evidence that the larvae of this genus are not adapted to a pelagic life as prolonged as those of the related genera, *Quietula*, *Clevelandia*, and *Ilypnus* (but not *Eucyclo-*

gobius). This conclusion is based on differences in postlarval pigmentation and behavior. Pelagic larvae and nektonic postlarvae characteristically are translucent with scattered melanophores, while the completely pigmented condition is found first in the benthonic stage. Postlarvae of *Gillichthys mirabilis* as small as 8–12 mm in length often are relatively heavily pigmented. At a comparable length, postlarvae of the other genera mentioned above are much more translucent.

Postlarvae of *mirabilis* in a slough in the northern Gulf of California, and at the Salton Sea, were seen to drift or swim into the current in slowly moving water. The postlarvae descended to the bottom and held station when the current strength increased. Postlarvae of *Quietula guaymasiae* Jenkins and Evermann were observed to form small groups that swam vigorously in a strong tidal current in the Gulf, darting from side to side at the surface in a manner reminiscent of young atherines; they seemed well adapted for life in open water. The larvae of *Gillichthys mirabilis* evidently are not dispersed as readily as are those of the related genera just mentioned.

Reproduction

Spawning apparently commences in January throughout the range of *mirabilis*, but the length of the season is uncertain. In southern California spawning takes place throughout the

period from January to July (Weisel, 1947: 82). My observations indicate that spawning also starts in January in the Alviso ponds; females hatched there in January and February, however, are mature and full of ripe eggs in August and September of the same year. It is

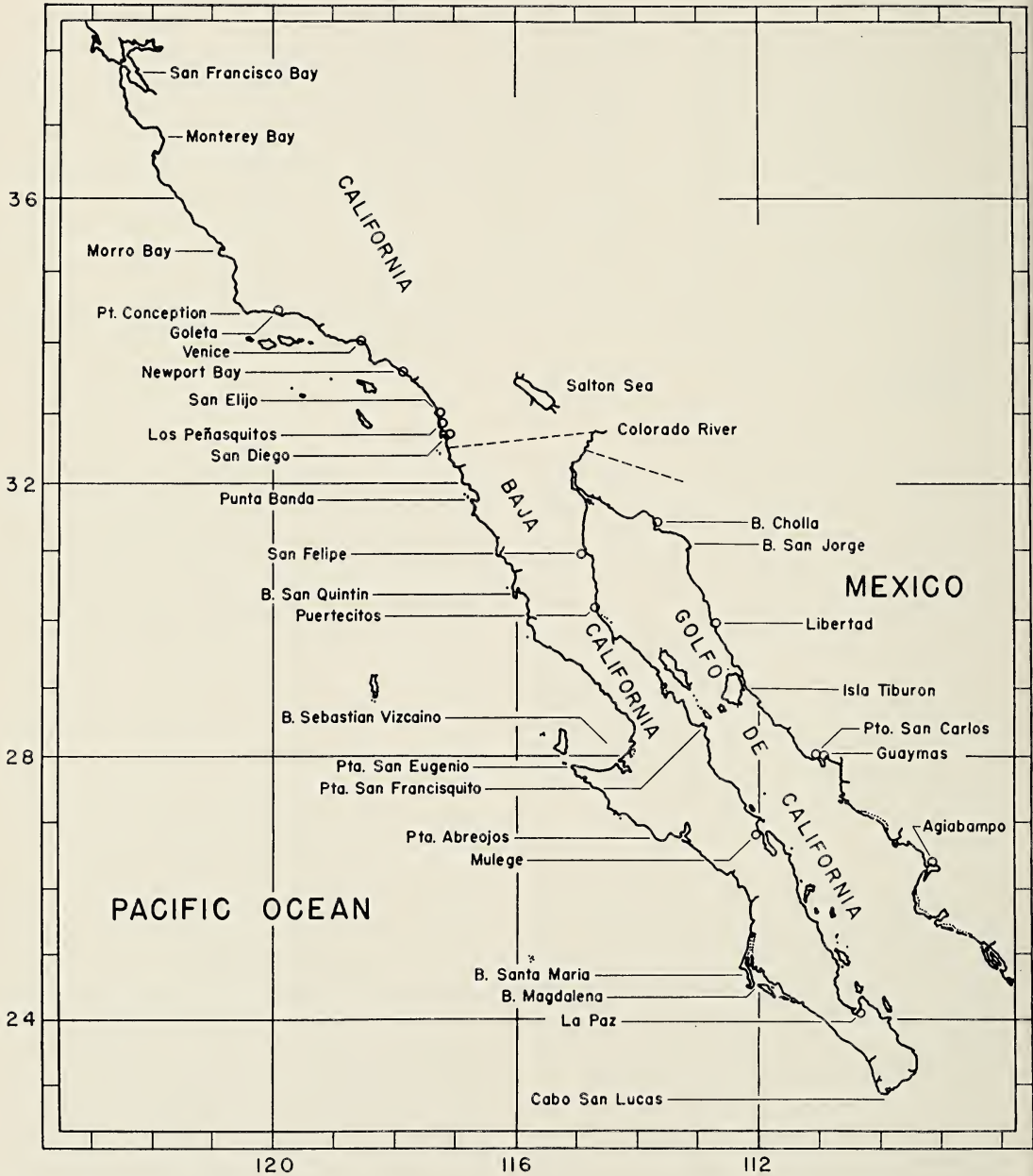


FIG. 1. Chart of the study region; latitude N, longitude W.

not known whether or not they spawn this late in the season. In the Salton Sea, the first spawning occurs in January and the last in May or June. Postlarvae of *mirabilis* have been collected in early February in the northern and central Gulf of California. There are no data available on the length of the spawning season in Gulf populations.

Depending on the size of the female, 4,000–9,000 eggs are laid at each spawning (Weisel, 1947: 80). Weisel believed that each female spawns once, rarely twice, in a season. Examination of ovaries of Salton Sea fish leads me to believe that each female *mirabilis* oviposits 2 or 3 times each season, with an interval of 40–50 days between spawnings. MacGinitie (1939: 500) reported that the related blind goby, *Typhlogobius californiensis* Steindachner, spawns twice during one season, with an interval of about 2 months. Females of a more distantly related goby, the mapo, *Bathygobius soporator* (C. and V.), can repeat a spawning in 7–16 days (Tavolga, 1954: 432). If the above estimates are correct, each female *Gillichthys mirabilis* has a potential production of about 8,000–27,000 eggs in one season.

The young of *mirabilis* reach maturity by the end of their first year. Rate of growth was investigated only at the Salton Sea. It is clear from these data and from the changes in size composition of collections from other locations taken at different times of the year, that most fish attain adulthood and a standard length of 100–140 mm by the end of their first year. Nothing is known of their life expectancy.

MATERIALS AND METHODS

In the preliminary analysis of *mirabilis* and *seta*, certain counts and measurements were selected as being especially promising (Barlow, 1961a). While investigating these, other useful characters also came to light.

All counts and measurements, except one, were carried out in accordance with the methods of Hubbs and Lagler (1949). The exception, the height of the anal fin, is defined here as the distance from the base of the last element of the anal fin to the tip of the second to last ray, when the fin is erect.

The study was based almost entirely on specimens deposited in the Fish Collections of the University of California, Los Angeles. About 4,000 specimens of *mirabilis* were examined. The fish from San Francisco Bay (Alviso ponds) were obtained from Sim's Bait Shop, Long Beach, California, and care was taken to verify the original source of this material. After fixation in 10% formalin, the specimens were washed and placed in 46% isopropyl alcohol.

Statistical Methods

The purpose of each statistical test in this paper is solely to accept or reject a hypothesis. The decision to accept or reject a hypothesis was based on the 5% critical level, to minimize type II errors (Hoel, 1954: 33). Acceptance of a hypothesis such as equal means, however, merely indicates no detectable differences and does not imply that the populations in question are proven to be the same. Critical values usually are given; the subscript notation 0.95 refers to a one-tail test, and 0.975 to a two-tail test.

Four kinds of tests were employed. The F-test was used when the hypothesis involved the testing of two variances. Covariance was applied to problems when two or more regressions (fitted by least squares) were tested at the same time. Decisions to accept or reject differences between two means were determined by *t*-tests. Correlation coefficients were evaluated as outlined by Hoel (1954: 124).

Obvious differences were not tested. When several variances or means were compared, the two most divergent values were examined first. If no significant differences were revealed, the others were not tested.

The statistical parameters of the fin ray counts are presented graphically. The format is that of Hubbs and Hubbs (1953). Unless the separation between means was patent, no statistical inferences have been drawn from these figures.

RESULTS

Head

The head of fish from the Gulf of California, as seen from the side, is more pointed than in Pacific Coast specimens. In this respect the Gulf populations approach *seta*. The difference in

TABLE 2
FIN COUNTS FOR *Gillichthys mirabilis*, MATERIALS AND LOCALITIES

°N	LOCALITY	COLLECTED	FIN COUNTS n (SIZE RANGE)
Pacific Coast			
37°27'	San Francisco Bay	June 1957	30 (39-86)
35°20'	Morro Bay	August 1957	30 (86-132)
34°24'	Goleta	September 1957	30 (64-125)
34°00'	Venice	June 1957	28 (83-138)
33°37'	Newport Bay	October 1955	25 (56-154)
33°01'	San Elijo Lagoon	June 1956	30 (58-142)
32°47'	Mission Bay	May 1946	30 (38-54)
31°43'	Estero Punta Banda	July 1955, 1956	20 (80-124)
30°30'	Bahia San Quintin	July 1956	14 (91-142)
26°45'	Punta Abreojos	May 1948	16 (10-20)
24°47'	Bahia Sta. Maria	April 1955	30 (22-38)
Salton Sea			
33°18'	NW Shore	July 1953 ¹	30 (55-109)
	NE Shore	July 1954 ¹	30 (40-78)
	NW Shore	July 1955	30 (35-74)
Gulf of California			
31°21'	Bahia Cholla	January 1949	30 (20-30)
	Bahia Cholla	April 1954	30 (48-88)
31°18'	San Felipe	April 1957	31 (25-50)
27°57'	Estero Soldado	January 1952	31 (15-20)
26°54'	Mulege	March 1957	30 (35-50)
26°22'	Bahia Agiabampo	January 1951	10 (66-100)

¹ Not included in Figures 6-12.

shape is due largely to the more depressed head of the Gulf fish, and was one of the main reasons for naming this form as a new species. In their description, Gilbert and Scofield (1898: 498) commented on the depressed head of *Gillichthys detrusus* (= *G. mirabilis* Cooper). This condition prevails in all the populations investigated from the Gulf. The mean head depth for fish from "El Marino" slough, just north of San Felipe, is 15.6% (13-18%; $n = 10$) of standard length, which agrees nicely with the value for Bahia Agiabampo fish (Barlow, 1961a). It should be noted at this point that the position of the opercles and the branchiostegals of preserved gobies can cause considerable variation in measurements of head depth and especially of head width.

The head shape of Salton Sea fish is more like that of specimens from the Pacific Coast than of those from the Gulf. The measured head depth, though, is closer to that of Gulf populations (Barlow, 1961a).

The regression of head length on standard length is slightly, but significantly, greater for the Pacific Coast populations than for the fishes from the Gulf when the data are pooled (Fig. 2, Table 3). Along the Pacific Coast the five populations also differ significantly from one another (Table 3). The differences between Gulf populations are of approximately the same degree as those between the Pacific Coast groups, but this was not tested statistically. Fish from the Salton Sea have the shortest heads, which is immediately noticeable when inspecting large adults.

Relative growth differences are seen best by plotting the logarithms of head and standard length (Martin, 1949: 8). The regressions for all populations so presented are nearly parallel (no figure). These curves for relative growth of the head, however, are slightly but clearly curvilinear; the slopes steepen with increasing standard length. The relative degree of difference between any of the lines is the same for the

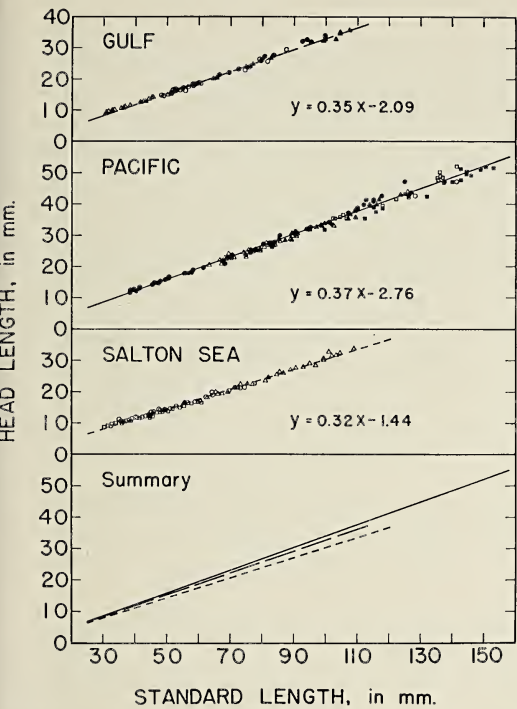


FIG. 2. Head length versus standard length. Gulf of California populations: open triangle, San Felipe (El Marino); open square, Mulege; open circle, Bahia Cholla, 1954; closed triangle, Guaymas (Estero Bocochibampo); closed circle, Agiabampo. Pacific Coast populations: closed circle, San Francisco Bay (Alviso ponds); open triangle, Goleta; closed square, Newport Bay; open circle, San Elijo Lagoon; closed triangle, Estero Punta Banda; open square, Bahia San Quintin. Salton Sea population: open triangle, 1953; open circle, 1954; open square, 1955.

smallest and largest fish measured, i. e., the lines are parallel. Therefore, differences between slopes of arithmetic plots presented here are of no biological significance.

Upper Jaw

The analysis of upper jaw measurements is complicated by the curvilinear relationship between jaw length and standard length. (Hereafter, upper jaw is referred to as jaw.) This difficulty is alleviated somewhat by fitting two regressions through the data: one line for fish greater than 90 mm, and another for the smaller specimens (Fig. 3). The change in slope is an artifact of the arithmetic plot; relative growth is only slightly curvilinear. The situation is also

complicated by the sexual dimorphism of jaw length in adult fish. The average length of the jaw is slightly greater in males, even though the range is about the same in both sexes. Consequently, the results of the covariance tests (Table 3) should be regarded with skepticism, since some of the assumptions underlying the test are not entirely satisfied.

The jaw of fish from the Gulf is about equal to, or slightly larger than, the jaw of Pacific Coast fish when specimens of the same length are compared. On the same basis, the jaw is much shorter in fish from the Salton Sea.

If jaw lengths are compared as a function of head length instead of standard length, the jaw is still relatively longest in Gulf fish and shortest

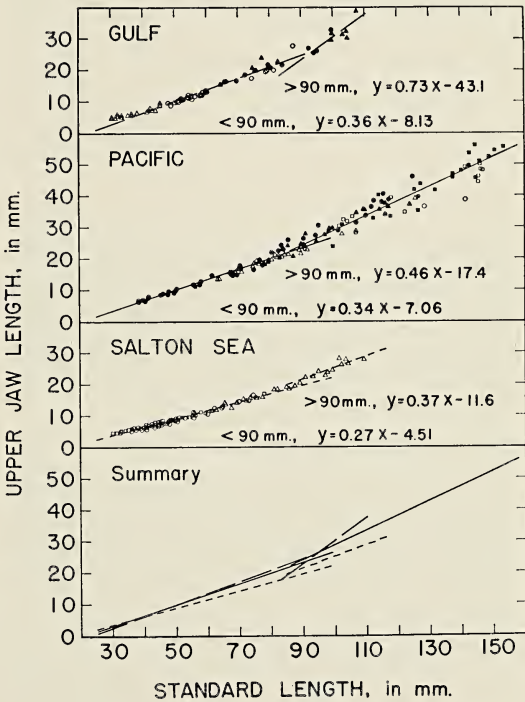


FIG. 3. Upper jaw length versus standard length. Gulf of California populations: open triangle, San Felipe (El Marino); open square, Mulege; open circle, Bahia Cholla, 1954; closed triangle, Guaymas (Estero Bocochibampo); closed circle, Agiabampo. Pacific Coast populations: closed circle, San Francisco Bay (Alviso ponds); open triangle, Goleta; closed square, Newport Bay; open circle, San Elijo Lagoon; closed triangle, Estero Punta Banda; open square, Bahia San Quintin. Salton Sea population: open triangle, 1953; open circle, 1954; open square, 1955.

TABLE 3

RESULTS OF CO-VARIANCE TESTS ON DIFFERENCES IN MORPHOLOGY OF *Gillichthys mirabilis*
(Hypothesis tested is equal means after adjustment for standard length.
Key: F, F ratio; d.f., degrees of freedom; F_{.95}, 5% critical value.)

	F	d.f.	F _{.95}	DECISION
Head length				
Gulf/Pacific/Salton Sea	80.3	2,299	3.03	reject
Gulf/Pacific	8.87	1,201	3.89	reject
Pacific (5 populations)	14.8	4,128	2.44	reject
Salton Sea (1953-55)	10.1	2,97	3.09	reject
Salton Sea (1954-55)	3.36	1,66	3.99	accept
Upper jaw length				
> 90 mm				
Gulf/Pacific/Salton Sea	10.6	2,87	3.10	reject
< 90 mm				
Gulf/Pacific/Salton Sea	41.6	2,208	3.04	reject
Salton Sea (1953-55)	7.99	2,84	3.10	reject
Salton Sea (1954-55)	< 0.58	1,66	3.99	accept
Anal fin height				
Gulf/Pacific/Salton Sea	37.8	2,291	3.03	reject
Pacific (6 populations)	19.1	5,129	2.29	reject
Salton Sea (1953-55)	3.13	2,95	3.10	reject

in those from the Salton Sea. The jaw is 81, 74, and 71% of head length for Gulf, Pacific Coast, and Salton Sea fish, respectively. Thus, the jaw of the Salton Sea fish is shorter in regard to head length as well as standard length.

Median Fin Height

The soft dorsal and the anal fins are higher in fish from the Gulf than in those from California and the Salton Sea (Barlow, 1961a, table 1). Only the variation in anal fin height is reported in detail.

The anal fin height varies significantly from population to population along the Pacific Coast (Fig. 4, Table 3). San Francisco fish, for instance, often fall below the fitted regression; Newport Bay and Estero Punta Bunda specimens usually are above it. The data are too few to make an unequivocal statement about trends, but the fins of northern fish tend to be lower than those from the south.

Gilbert and Scofield (1898: 498) mentioned the higher anal fin of *detrusus* (= *mirabilis* Cooper) when they described it as a new species.

The type locality is the tidal region of the Colorado River delta, but high anal fins are also typical of the populations to the south in the Gulf (Fig. 4). The regression of fin length on standard length for Gulf forms is higher and steeper than those for the populations from the Pacific Coast and the Salton Sea. The variation between Gulf populations is assumed to be significant. No trend with latitude is apparent.

One sample from the northwestern region of the Gulf (an isolated salt pond 25 km north of San Felipe) has remarkably low median fins, and the dorsal fin profile is less rounded than in the typical Gulf form (Fig. 5). The height of the anal fin averages 8.8% (8.3-9.5%) of the standard length (based on 10 specimens, 61-102 mm in length). Thus the anal fin height and the dorsal fin shape resemble those of fish from the Pacific Coast. These data were not included in the regression of fin height versus standard length because the specimens had not been examined at the time the calculations were carried out and the figure was prepared. The fish of this population are thought to be not representative of the usual Gulf condition.

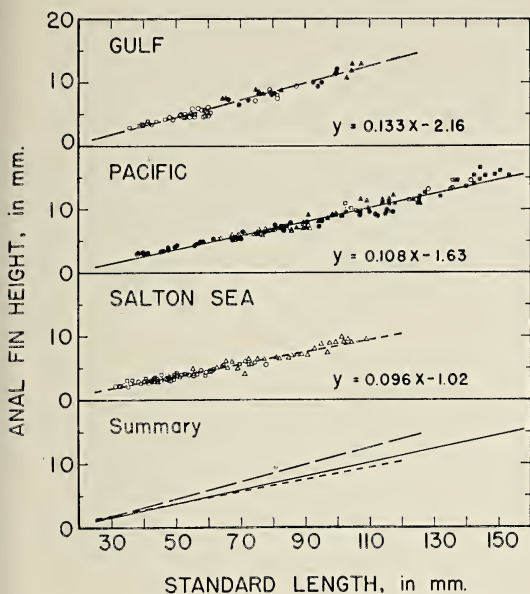


FIG. 4. Anal fin height versus standard length. Gulf of California populations: open triangle, San Felipe (El Marino); open square, Mulege; open circle, Bahia Cholla, 1954; closed triangle, Guaymas (Estero Boco-chibampo); closed circle, Agiabampo. Pacific Coast populations: closed circle, San Francisco Bay (Alviso ponds); open triangle, Goleta; closed square, Newport Bay; open circle, San Elijo Lagoon; closed triangle, Estero Punta Banda; open square, Bahia San Quintin. Salton Sea population: open triangle, 1953; open square, 1954; open circle, 1955.

The anal fin height of Salton Sea fish (Fig. 4) is considerably lower than in Gulf groups. Compared to Pacific Coast populations, the fin heights are similar but nevertheless lower. The variation in height from year to year in the Salton Sea fish is just significant at the 5% level.

The profile of the second dorsal fin is more rounded in specimens from the Gulf of California than in those from the outer coast or the Salton Sea. This results from the relatively greater increase in length of the centermost rays in the higher fins. Besides the change in shape, the anterior height of the second dorsal fin equals or exceeds that of the first dorsal in Gulf forms (Gilbert and Scofield, 1898: pl. 38). In fish from the Pacific Coast and the Salton Sea, the anterior rays are lower and the central rays are equal to or only slightly higher than the spiny dorsal.

Distance between Dorsal Fins

The distance between dorsal fins is greatest in fish from the northern part of the Gulf of California, ranging from 1.0 to 1.8 times the eye diameter. The distance between fins of specimens from the central and southern Gulf is about the same as that of fish from central California, being 0.7–1.1 times the eye diameter. The distance between dorsal fins was one of the diagnostic characters used by Gilbert and Scofield (1898: 498) to separate *detrusus* from *mirabilis*.

In Salton Sea fish, the distance between fins is less than one eye diameter. The posterior margin of the first dorsal sometimes touches the anterior margin of the second dorsal. A greater number of elements in both dorsal fins as well as an encroachment on the space by two to three supernumerary spines on the leading edge of the second dorsal fin cause the decrease in distance.

Squamation

The scales are slightly larger in specimens of *mirabilis* from the Gulf of California than they are in those from the outer coast and the Salton Sea. The counts range from 60 to 80 irregular vertical rows of scales along the body in Gulf forms, while there are about 80–100 rows in fish from the Pacific Coast and the Salton Sea.

The ventral squamation is more extensive in fish from the Gulf than in those from the Pacific Coast or the Salton Sea. The scales extend anteriorly around the base of the pelvic fin in about 30% of the specimens from Bahia Agiabampo (southern Gulf), in about 10% from Guaymas (central Gulf), and in about 80% from Bahia Cholla (northern Gulf). In fish from the Pacific Coast, the scales only occasionally reach anteriorly beyond the lateral insertion of the pelvic fin base.

In many respects the scalation is less extensive in Salton Sea fish, although the scales are about the same size as those on fish from the Pacific Coast. The ventral, anterior margin of the scaled area usually just reaches the insertion of the pelvic fins, but not beyond. The scaleless area directly under the pelvic fins is greater than in naturally occurring populations. The naked

area extends posteriorly to just beyond the tip of the pelvic fins but is not as wide as the pelvic fins; the size of the area is variable but is always larger than in other populations. A vertical strip in the axil, about one-half an eye diameter wide, is also without scales. Further, the strip of scales on the nape is shorter than in the other populations (Barlow, 1961a). The base of the caudal fin rays has two to six vertical rows of scales on it. In this respect only, the Salton Sea fish occasionally are more fully scaled than those of the other populations.

First Dorsal Fin

The average spine number is about six for all populations, although some means deviate appreciably from this value (Fig. 6). The count never was found to be less than six in Gulf populations. Five spines, however, are not uncommon in other populations. The only geographic trend discernible concerns the variances of the populations; this is reported below.

Second Dorsal Fin

The mean number of rays in the second dorsal fin is clearly higher in Pacific Coast than in Gulf populations (Fig. 6). On the Pacific Coast the counts are lower in the south, while in the Gulf the counts are more nearly uniform, or slightly higher in the south. Thus the average number of fin rays for Gulf and Pacific Coast

populations tends to converge in the lower latitudes.

The mean number of dorsal fin rays in the Salton Sea population is greater by about one ray than in the other populations.

The large range and variation of the Newport Bay population are caused chiefly by one specimen with only eight rays. The fin does not look aberrant but it must be considered atypical.

Anal Fin

On the Pacific Coast the mean number of anal fin rays increases from the north, south to San Diego, then decreases further south. In the Gulf, where samples are less complete, the means are about the same in all populations, or are a little higher in the south. The means of the Gulf and Pacific Coast populations converge in the lower latitudes (Fig. 7).

The mean number of anal fin rays in the fish from the Salton Sea is conspicuously higher than in any of the naturally occurring populations (Fig. 7).

Pectoral Fin

The mean number of pectoral fin rays increases progressively from north to south on the Pacific Coast, but in the Gulf of California the average number decreases to the south. Consequently, the means of Pacific Coast and Gulf

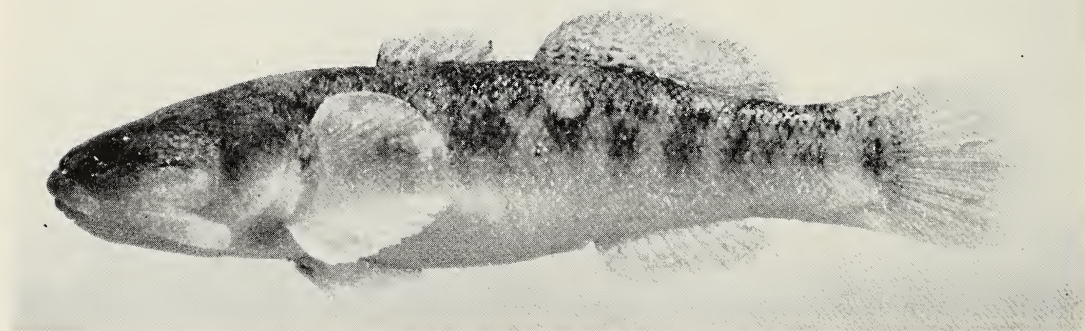


FIG. 5. *Gillichthys mirabilis*, female, standard length 100 mm, from "El Marino" slough north of San Felipe, Baja California. The small black spot on the side of the specimen is a blemish.

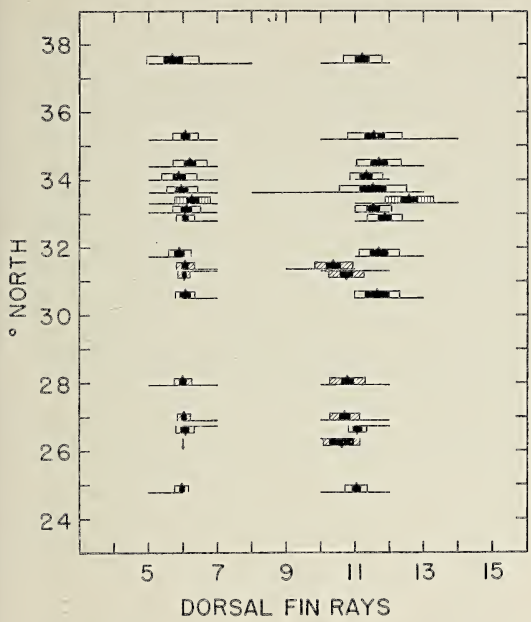


FIG. 6. Fin rays in the first (spiny) and second (segmented only) dorsal fins, from left to right, presented as a function of °N latitude. Materials and place names in Table 2. Large rectangle, one standard deviation on either side of mean (triangular prominence); blackened space, two standard errors on either side of mean; lower horizontal line, range of counts. Open rectangle, Pacific Coast populations; vertical lines in rectangle, Salton Sea population; oblique lines in rectangle, Gulf of California populations.

populations overlap in the southern latitudes (Fig. 8).

The average pectoral fin count of the Salton Sea fish again is much higher than in Pacific Coast animals. The number of fin rays, however, is similar to that found in northern Gulf populations (Fig. 8).

The Venice population, near Los Angeles on the Pacific Coast, is extremely variable. Some pectoral fins are deformed and obviously are aberrant. This habitat is polluted by sewage and industrial waste products.

Combined Fin Counts

Some of the trends and differences observed in the study of individual fins disappear when the fin counts are combined and plotted as a function of latitude (Fig. 9). At different latitudes the averages of the combined fin counts

are about the same, except in California where a slight increase from north to south occurs. Otherwise there is no trend in the mean number with latitude. When comparisons are made at the same latitudes, the Pacific Coast populations and all of the Gulf populations, except for San Felipe, broadly overlap. Contrariwise, some divergences are enhanced. The Salton Sea and San Felipe populations are obvious deviants. Further discussion of combined fin elements is reserved for the section on annual variation.

Fin Ray Variance

Over the geographic range of *mirabilis* there are dissimilarities in the variances of each of the fins. The difference between the extreme variances of the first dorsal fin on the Pacific

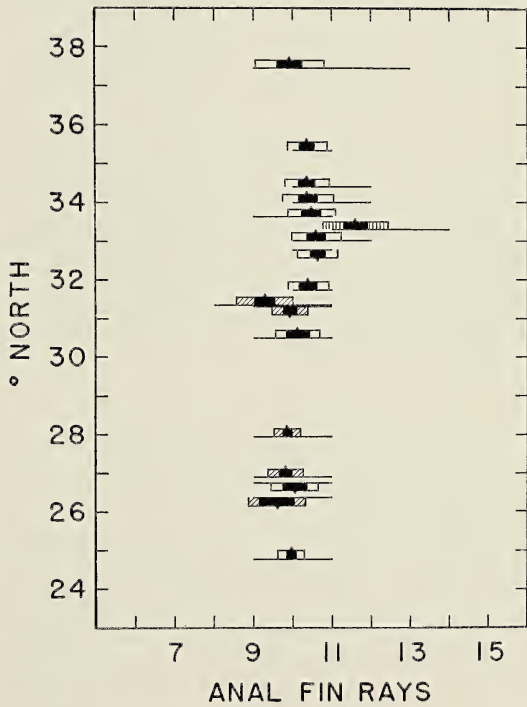


FIG. 7. Fin rays in the anal fin (segmented only) presented as a function of °N latitude. Materials and place names in Table 2. Large rectangle, one standard deviation on either side of mean (triangular prominence); blackened space, two standard errors on either side of mean; lower horizontal line, range of counts. Open rectangle, Pacific Coast populations; vertical lines in rectangle, Salton Sea population; oblique lines in rectangle, Gulf of California populations.

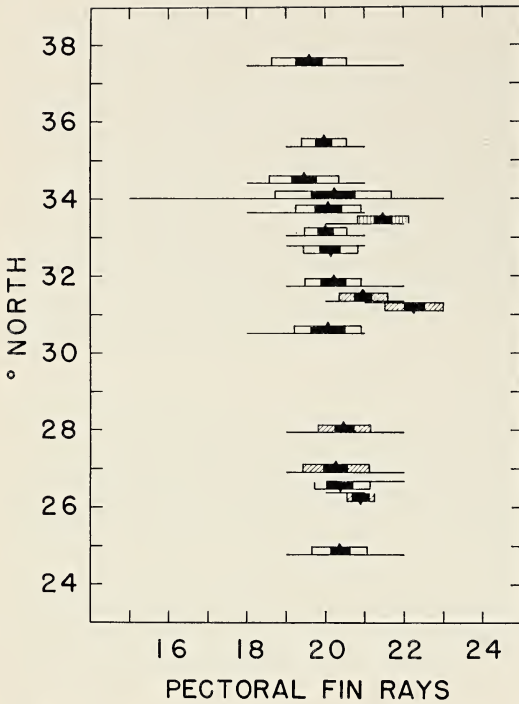


FIG. 8. Fin rays in the left pectoral fin presented as a function of °N latitude. Materials and place names in Table 2. Large rectangle, one standard deviation on either side of mean (triangular prominence); blackened space, two standard errors on either side of mean; lower horizontal line, range of counts. Open rectangle, Pacific Coast populations; vertical lines in rectangle, Salton Sea population; oblique lines in rectangle, Gulf of California populations.

Coast (San Francisco Bay and Bahia Santa Maria), for instance, is highly significant: $F = 16.9$, $F_{0.975}(29, 29) = 2.1$.

The intrinsic variability in the number of elements in a given fin is associated with the latitude where the population is situated. Increasing variability is associated with higher latitudes (Fig. 10). All the fins manifest this increase in variability from south to north, though not equally well. If one were to rate the correlations subjectively from good to poor, they would stand in the order (1) first and second dorsal fins, (2) combined counts, (3) anal fin, and (4) pectoral fin. Only the data from the first dorsal fin are presented here (Fig. 10); the other data are available on request. There also may be a positive correlation

between latitude and variance of the vertebrae (see below).

The correlation between degrees of latitude and variance of the first dorsal fin has a coefficient of 0.848, which differs significantly from a coefficient of zero. This high degree of correlation doubtless could be increased further by reducing that portion of the intra-population variation resulting from sampling techniques, thereby improving the estimate of the real variance. As will be seen further on, comparisons of relatively homogeneous year classes from succeeding years show that even though the mean number of elements in the various fins may change, the variance remains the same. Some

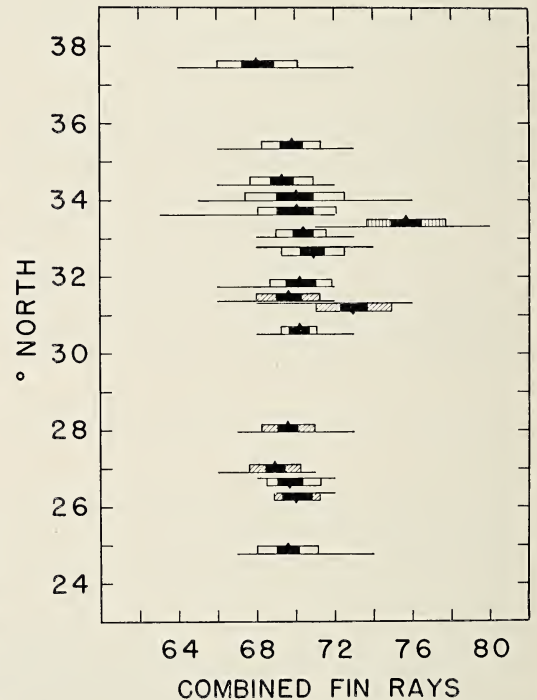


FIG. 9. Combined elements, segmented and unsegmented, in the first and second dorsal, anal, and left and right pectoral fins, presented as a function of °N latitude. Materials and place names in Table 2. Large rectangle, one standard deviation on either side of mean (triangular prominence); blackened space, two standard errors on either side of mean; lower horizontal line, range of counts. Open rectangle, Pacific Coast populations; vertical lines in rectangle, Salton Sea population; oblique lines in rectangle, Gulf of California populations.

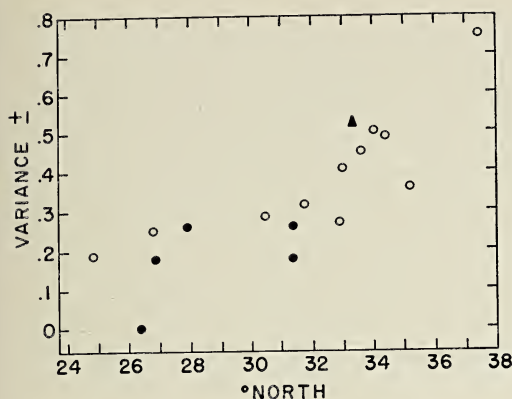


FIG. 10. Correlation between population variances ($\pm$) of the first dorsal fin, and °N latitude. Open circle, Pacific Coast populations; closed triangle, Salton Sea population; closed circle, Gulf of California populations.

of the samples represented by a single value in Figure 10 are heterogeneous, consisting of more than one year class. Similar dispersion in each year class, but about different means, would increase the apparent variation.

Fin Ray Correlations

The segmented rays of the dorsal and anal fins are positively correlated. When all the counts are combined, exclusive of the Salton Sea, the correlation coefficient is 0.603, significantly greater than zero. A positive correlation also is evident within and between year classes.

The number of elements in the pectoral fin compared to that of the anal, and of the soft dorsal fin, reveals negative correlations, but only when means of different populations are compared (Fig. 11). The correlation coefficient for the pectoral fin with the second dorsal fin is -0.737 , and with the anal fin it is -0.659 ; both values differ significantly from zero. The data for the sample from San Felipe are shown in Figure 11 (the highest pectoral fin mean) but are not included in the computations of the correlation coefficients; as mentioned before, the counts are atypical. The inclusion of these counts does not affect the conclusion that the pectoral and median fin counts are significantly correlated. Data from samples from the Salton Sea also are not included.

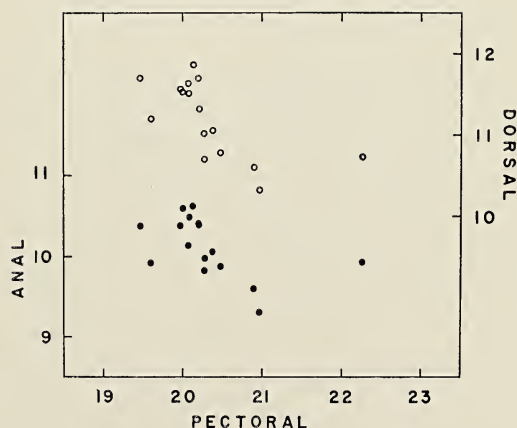
Fin Ray Index

Probably the most useful statistic obtained from the fin counts is a derived index. The soft rays of the dorsal and anal fins are summed, then divided by the number of rays in the left pectoral fin and multiplied by 100. This index reflects the change in relationship between the fin ray numbers of pectoral and median fins at different latitudes (Fig. 12).

On the Pacific Coast, not including San Francisco and Venice, the index decreases progressively from north to south. In the Gulf of California the opposite is the case; the index increases to the south. The indices of Gulf and outer-coast populations consequently converge at low latitudes, being slightly higher in outer-coast populations.

Noteworthy is the excellent agreement of index values for samples from Bahia Cholla and San Felipe, situated at similar latitudes but on opposite coasts of the Gulf. This is especially striking, considering that the San Felipe fish have unusually high atypical counts.

The most revealing index is that of the Salton Sea population. It agrees with values obtained from samples taken in the vicinity of San Diego, the source of the Salton Sea stock. Further, the index is considerably higher than in any of the Gulf populations.



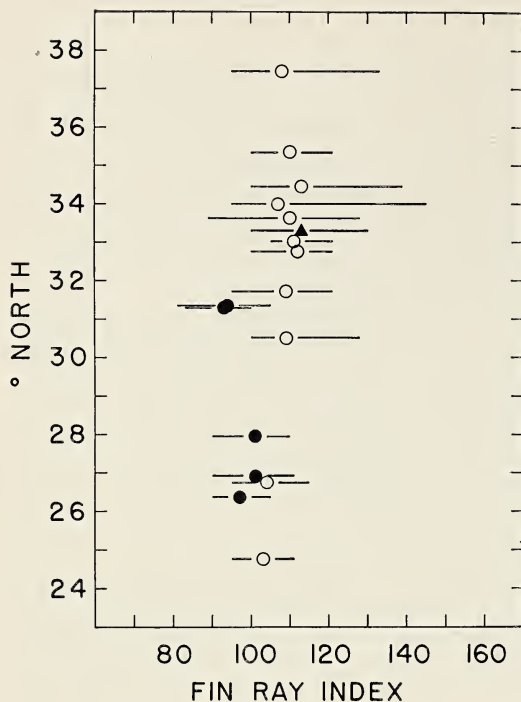


FIG. 12. Fin ray index: combined number of segmented rays in the second dorsal fin and anal fin, divided by the number of rays in the left pectoral fin, multiplied by 100. Open circles, means of Pacific Coast populations; closed circles, means of Gulf of California populations; closed triangle, mean of Salton Sea population; horizontal lines, ranges of values.

Pectoral Fin Asymmetry

Species of fishes are known to differ in degree of asymmetry between the number of elements in the right and left pectoral fins (Hubbs and Hubbs, 1945). The numerical asymmetry between right and left pectoral fin counts in *mirabilis* was investigated to determine if individual populations, or geographic regions, could be characterized by this feature (Table 4). Only the total amount of asymmetry, right plus left, was found to be useful in this respect. Values for the Pacific Coast and Salton Sea populations are usually higher (mean about 30%) than those from the Gulf (mean about 20%). The amount of asymmetry in the two most southerly populations on the Pacific Coast, however, is the same as that of the Gulf forms.

The degree of asymmetry is equally divided between right and left. To facilitate comparisons, each population can be characterized according to whether there are more fish with higher counts in the right fin than in the left fin, or vice versa. If a sample has more fish with right fins of a higher count than the left, it is tallied as a "dextral"; and with more lefts than rights, as a "sinistral."

Among collections from the Pacific Coast 5 out of 11 are dextral. In the Gulf, 3 out of 6 are dextral, 1 is sinistral, and 2 are equal. The Salton Sea population vacillates from year to year between dextral and sinistral. Therefore, the distribution of rights and lefts within and between populations is typical of a 50-50 chance situation, such as the toss of a coin.

Vertebrae

The number of vertebrae was compared in five populations (Table 5). In every sample the mode is 32, and the average is approximately the same value. Only the mean of the Salton Sea specimens differs appreciably from 32; it is significantly higher ($t = 2.02$; $t_{0.95} (29) = 1.70$).

In contrast to the relative uniformity of the means, there are patent differences between the variances; they are greater in the Salton Sea and Pacific Coast groups than in those from the Gulf. Each of the variances of the San Francisco and Salton Sea samples was tested against that of the northern Gulf collection; the F-ratios are $F = 13.6$, $F_{0.975} (18, 39) = 2.4$, and $F = 8.6$, $F_{0.975} (29, 39) = 2.1$, respectively. The variances of the San Francisco and Salton Sea groups are not significantly different: $F = 1.6$, $F_{0.975} (18, 29) = 2.5$.

The variances of the vertebrae decrease from high to low latitudes. If the variances are listed from north to south, instead of as shown in Table 5, the following series of values is obtained: 0.577, 0.461, 0.182, 0.157, 0.341, 0.0. Considering the few populations represented, the correlation is surprisingly good. The presence of a similar positive correlation between latitude and fin ray variance (see above) increases the confidence in the trend indicated by the variances of the vertebrae.

Annual Variation

Material for the study of annual variation came from the Salton Sea and from Bahia Cholla (northern Gulf of California). Each sample was from a year class hatched in the year considered. This affords a rough estimate of the stability of the statistical parameters used in the comparison of separate populations.

The Salton Sea was sampled during the same month on three successive years. The fish of one sample are larger than the others (Table 6) and probably were hatched earlier in the year than those of the other two samples. In addition, the 1954 collection was from a different part of the Sea, but I doubt that this is of importance. Both body measurements and fin counts were taken.

The two samples from Bahia Cholla came from year classes that had hatched under strik-

ingly different temperature conditions. The first were embryos during an unusually cold period late in the winter of 1949. A moderate fish kill occurred in the northern Gulf at that time. The second collection, 1954, consists of fish that had developed in a relatively normal temperature situation. Only counts were taken because the specimens are small.

Slight, but significant, differences occur between the means of fin counts of different year classes from the Salton Sea (Table 6). In the 1955 class, all counts are higher than in the previous two years (except for the first dorsal fin: 1955 vs. 1953, $t = 0.67$, $t_{0.95} (58) = 1.67$). The mean of the second dorsal fin exceeds that of the anal fin by about one ray in each year class.

The ratios of median fin rays to pectoral rays, as indicated by the fin indices, remain approximately the same. Thus while the means

TABLE 4
BILATERAL ASYMMETRY OF PECTORAL FINS
ARRANGED BY REGIONS, FROM NORTH TO SOUTH

AREA	n	PERCENTAGES		
		L > R	R > L	R + L
Pacific Coast				
San Francisco	30	17	20	37
Morro Bay	30	23	10	33
Goleta	30	10	27	37
Venice ¹	28	29	25	54
Newport Bay	25	4	12	16
San Elijo Lagoon	30	13	23	36
Mission Bay	30	3	13	16
Estero Pta. Banda	20	25	10	35
Bahia San Quintin	14	14	21	35
Pta. Abreojos	16	19	6	25
Bahia Sta. Maria	30	13	3	16
Salton Sea				
1953	30	17	13	30
1954	30	7	10	17
1955	30	20	13	33
Gulf of California				
Bahia Cholla—1949	30	10	17	27
Bahia Cholla—1954	30	10	10	20
San Felipe	31	10	3	13
Estero Soldado	31	13	16	29
Mulege	30	10	10	20
Bahia Agiabampo	10	0	10	10

¹ Aberrant; see pectoral fin section.

TABLE 5
VERTEBRAL COUNTS FOR *Gillichthys mirabilis*
(Key: x, mean; s, one standard deviation.)

AREA	YEAR	NO. OF VERTEBRAE			STATISTICAL PARAMETERS		
		31	32	33	n	x	$\pm s$
Pacific Coast							
San Francisco	1955	3	13	3	19	32.00	0.577
Pta. Abreojos	1948	2	14	1	16	31.88	0.341
Gulf of California							
Bahia Cholla	1949	—	29	1	30	32.03	0.182
San Felipe	1955	—	39	1	40	32.03	0.157
Est. Soldado	1952	—	30	—	30	32.00	0
Salton Sea	1955	1	23	6	30	32.17	0.461

of fin ray counts may change, the relationships between them are relatively unaffected.

The divergence of means between the year class samples from Bahia Cholla is greater than that recorded in the Salton Sea material. The mean number of rays for each fin, except the first dorsal, is higher in the "cold" year than in the "normal" year fish. The differences are significant at the 5% critical level. The outstanding deviation is in the mean of the second dorsal fin which is higher by one full ray.

The relationship between the counts of the fin rays also is different in the 1949, or "cold" year class from Bahia Cholla. This results from the disproportionate increase of the soft dorsal fin count, which exceeds the anal fin by 1.7 rays. In most populations, as in the 1954 collection from Bahia Cholla, the average number of rays in the second dorsal fin surpasses that in the anal by only about one ray (0.8 to 1.3).

The fin index also reflects the change in the relationship between the fin counts. It is higher by 4% in the 1949 sample, probably due to the unusual rise in the number of dorsal fin rays.

Although the average number of fin rays and their interactions may change from year to year, the variance of each fin remains the same. F-tests were performed using the maximum and minimum variance of each fin within the year classes of each population; all F-ratios were below the 5% level of significance.

The direction of the annual variation in fin counts is of particular importance to conclusions

drawn later. In each instance when a year class deviates to a noticeable degree, the direction of the changes are the same for all fins with segmented rays. Increases in the dorsal and anal fin counts, as just shown, are paralleled by an increase in the number of pectoral fin rays; i.e., they are positively correlated. Within any one year class, however, there is no correlation whatsoever between the number of segmented rays in median fins and in the pectoral fins (Table 7). The pectoral fin counts are the same, on the average, whether a fish has many or few median fin rays, when from the same year class.

The bilateral asymmetry of the number of pectoral fin rays fluctuates between samples of year classes from the Salton Sea and from Bahia Cholla. Both the amount and the direction of the asymmetry vary (Table 4). The total asymmetry is maximal in the Salton Sea sample for 1955 and in the Bahia Cholla collection taken in 1949.

The head and jaw length and the anal fin heights are about the same in the three year classes collected from the Salton Sea. When the three groups are tested together, the differences are significant (Table 2), although the comparison of anal fin heights for all three samples just exceeds the 5% level of significance. If only the 1954 and 1955 samples are compared, the differences no longer are significant (Table 3). The size ranges of the 1954 and 1955 samples nearly coincide, while that from the 1953 year class contains larger fish. The inclusion in

the test of the sample with the larger fish apparently causes the significant differences between the groups. Hence the differences between the three year classes seem to be caused by unequal size groups.

Peculiarities of G. mirabilis from the Salton Sea

The *mirabilis* introduced into the Salton Sea differ from naturally occurring populations in several ways. Most of these differences seem to indicate an interference with the normal developmental physiology.

Some of the unusual features of the Salton Sea fish have already been discussed in earlier sections, and they are enumerated below. All the counts of fin rays and vertebrae are higher in these fish than in any others. The relationship between the fin ray numbers as reflected by the fin index, however, has remained the same as that of the parental stock. The squamation is

less extensive, and the head and upper jaw are disproportionately small. The formation of the interorbital pore is delayed.

The Salton Sea fish differ from naturally occurring forms in still other ways not yet described. The otoliths are much coarser and more opaque than those of specimens from the outer coast. The outline of the otoliths, as seen from either flat side, is less angular and is often almost round. The edges of the otoliths usually are only weakly crenulate or smooth, and the characteristic notch is indistinct.

In gobiid fishes, the segmented rays of the soft dorsal and anal fin typically are preceded by one slender spine. This holds for *mirabilis* in naturally occurring populations, with rare exceptions. Supernumerary spines, however, have been found on two specimens of *mirabilis* from San Elijo Lagoon and one from Newport Bay, and also on one specimen of *seta* from San

TABLE 6
ANNUAL VARIATION OF FIN COUNTS OF *Gillichthys mirabilis*
(Key: x, mean; s, one standard deviation; r, range.)

COLLECTED	SALTON SEA			GULF OF CALIFORNIA	
	NW Shore 18 July 1953	NE Shore 17 July 1954	NW Shore 13 July 1955	Bahia Cholla 27 January 1949	Bahia Cholla 27 April 1954
Size range in mm	55-109	40-78	35-74	20-30	48-82
n	30	30	30	30	30
First dorsal					
x	6.23	6.27	6.27	6.07	6.07
±s	0.504	0.451	0.521	0.255	0.253
r	(5-7)	(6-7)	(5-7)	(6-7)	(6-7)
Second dorsal					
x	12.43	12.33	12.57	11.33	10.37
±s	0.679	0.547	0.679	0.480	0.555
r	(11-14)	(12-14)	(11-14)	(11-12)	(9-11)
Anal					
x	11.27	11.33	11.60	9.60	9.30
±s	0.583	0.480	0.814	0.564	0.702
r	(10-12)	(11-12)	(11-14)	(9-11)	(8-11)
Pectoral (left)					
x	21.33	21.33	21.47	21.30	20.97
±s	0.679	0.480	0.628	0.625	0.616
r	(20-23)	(21-22)	(20-22)	(20-23)	(20-22)
Combined					
x	74.93	74.67	75.70	71.73	69.67
±s	1.68	1.18	1.95	1.53	1.65
r	(72-79)	(73-77)	(71-80)	(69-76)	(66-72)
Index					
x	112	111	113	98	94

TABLE 7

RELATIONSHIP BETWEEN THE PECTORAL FIN RAYS AND THE SUM OF THE SEGMENTED RAYS OF THE SECOND DORSAL FIN AND ANAL FIN IN *Gillichthys mirabilis*

DORSAL PLUS ANAL SEGMENTED RAYS	17	18	19	20	21	22	23	24	25	26	27
San Elijo Lagoon											
mean pectoral rays					20.0	20.0	20.0	20.0			
(n)					(9)	(10)	(9)	(2)			
Salton Sea											
1953											
mean pectoral rays						21.0	21.1	21.2	21.7	21.0	
(n)						(2)	(11)	(9)	(6)	(2)	
1954											
mean pectoral rays							21.5	21.1	21.2		
(n)							(17)	(8)	(6)		
1955											
mean pectoral rays						22.0	21.5	21.3	21.5	21.0	22.0
(n)						(1)	(11)	(6)	(8)	(2)	(2)
Bahia Cholla											
mean pectoral rays	21.0	20.0	21.0	21.0	21.0						
(n)	(1)	(1)	(10)	(15)	(3)						

Felipe. But in fish from the Salton Sea, the segmented rays of each of these fins are commonly preceded by two, or occasionally three, spines. When two spines are present in the soft dorsal or anal, the anterior-most spine is short. Usually it is less than one-half the length of the first segmented ray. Sometimes it is difficult to find the anterior-most supernumerary spine. In the soft dorsal only, the first of three spines is always short (usually a stub) and sometimes does not reach through the skin, while the second usually is moderately well developed and may be greater than half the length of the first segmented ray.

Supernumerary spines occur in the second dorsal fin more often than in the anal fin. In samples from 3 successive years (in each, $n = 30$), the percentages of the fins with extra spines are: second dorsal = 40, 13, and 33; anal = 10, 3, and 3. These data are from direct observations.

Photographs with X-rays revealed the presence of additional spines beneath the skin and of their basal elements. In one collection ($n = 30$, from 1955, but a different sample than the one mentioned in the preceding paragraph),

53% of the specimens have two spines in the soft dorsal and 10% have three (total = 63%). In the same sample, 13% of the fish have two spines in the anal fin, but none have three.

The situation is further complicated in that the number of spines does not always agree with the number of basals. Three specimens with only one spine in the fin have two basal elements. There is an additional basal anterior to the basal of the first, and only, spine. In two specimens, on the other hand, two spines share a single basal. In these cases, the first spine is merely a stub. In the specimens with three spines, three basals are found. Generally, elements are added anteriorly onto the anal fin, and especially the soft dorsal fin. This is done either by adding spines, basal elements, or both.

Axial deformities are conspicuous in fish from the Salton Sea (Fig. 13). Mostly they are situated anterior to the origin of the second dorsal fin. These are predominantly direct dorsal flexures, but may tend to right or left. Posterior to the first dorsal fin, the flexures are divided about equally between dorsal, lateral, and ventral. A few specimens have severe lateral flexures in the hypural plate (Fig. 13). More than one

flexure per fish is not uncommon. Photographs with X-rays indicate that the structure of the vertebrae has broken down at the apex of the more extreme curvatures. Whether there is a disintegration and/or fusion of the vertebrae is not clear from the photographs.

The occurrence of axial deformities increases during the hottest months of the year (Table 8). During July, the incidence of twisted specimens increases from around the usual 25% to 30%. The maximum occurs in the period of October to December. (The very high value for October is based on a small sample and therefore is subject to greater errors of random sampling. There is also a serious problem in obtaining a truly random sample, because of the sudden appearance of deformities in the young fish.)

Axial aberrations usually are manifest for the first time in subadults during August, the peak of the hot season. There is no relationship between size and incidence of deformities in these young fish. The deformities appear during the same period of time but not at a given size.

Axial deformities are also apparent in the sciaenid fishes that have been introduced into the Salton Sea. Here, too, anterior kyphosis seems to be prevalent.

Other abnormalities are seen in *mirabilis* but are not as common as the axial terata. These include forward projection of the lower jaw (Fig. 13), dermal flaps on the upper jaw, and pronounced elongation of individual rays in the median fins.

DISCUSSION

Body Form

Differences in size and shape are apparent in comparisons between various kinds of fishes from waters of different temperatures. Almost invariably in the Northern Hemisphere, the more northern representatives of a species or of a genus are larger than those to the south (Hubbs, 1926: 60; Vladykov, 1934: 120). The changes in body proportions have not been as thoroughly investigated, but some tentative generalizations can be made. Northern, slowly growing races of a species usually have smaller heads, eyes, maxillas, and fins than do their southern counterparts, although opposite effects are not uncommon (Hubbs, 1926: 62; Vladykov, 1934: 118; Martin, 1949: 23; and included references).

Morphological differences in *Gillichthys mirabilis*, as indicated by lines fitted to part lengths versus standard length, are apparent between the aggregates of populations from the Gulf of California and the Pacific Coast, and between the populations within these regions. There is no pattern among the regressions (length of parts on standard length) which might provide a clue to the nature of the differences. There is only the slightest tendency for the height of the anal fin to be greater in more southern populations of the Pacific Coast region.

The Gulf populations differ, for the most part, from those on the outer coast in the way one would predict for faster developing fish.



FIG. 13. *Gillichthys mirabilis*, female, standard length 101 mm, from the Salton Sea, California, and typical of extreme terata. Fold below the pectoral fin is from an incision.

TABLE 8
AXIAL DEFORMITIES IN *Gillichthys mirabilis*
FROM SALTON SEA

MONTH	TOTAL FISH	DEFORMED FISH	PERCENT DEFORMED
1955			
April	19	5	26
May	98	26	27
June	124	34	27
July	37	11	30
August	45	14	31
October	15	8	53
December	98	36	37
1956			
January	136	33	24
February	32	8	25

The Gulf fish have higher fins and longer jaws, the head is more depressed, and they tend to be more completely scaled ventrally and have slightly larger scales. The head is shorter, however. Except for the slightly shorter head length, the form of *mirabilis* from the Gulf is consistent with a hypothesis of rapid development. As seen in the fish from the Salton Sea, shorter head length is correlated with lower fins, shorter jaws, and reduced scalation, and presumably this has resulted from retarded development. If, as suggested, the Gulf fish differ morphologically because of faster development, then they should have longer, not shorter, heads. This contradiction probably stems from genetic differences.

No satisfactory explanation can be given for the distinctly greater distance between dorsal fins of the specimens of *mirabilis* from the upper Gulf as compared with the other populations. The form of the fish from the upper Gulf, however, resembles that of fish from the lower Gulf, except for the distance between dorsal fins. Environmentally induced changes usually manifest themselves in several ways, instead of being expressed in one character only. The increased space between dorsal fins, therefore, most likely has a genetic basis.

Countable characters

One of the commonly accepted generalizations in ichthyology is that the number of elements in serially repeated characters tends to

be greater at higher latitudes (Vladykov, 1934: 102). Hubbs (1922, 1926) argued that this relationship depends chiefly on the temperature of the water during early development; lower temperatures were thought to result in increasing numbers of elements, and higher temperatures in lower numbers. Local temperature conditions have been observed to be associated with the anticipated changes in counts (reviewed in Barlow, 1961*b*). Moreover, any factor of the environment affecting rate of development, such as salinity or oxygen tension, seems to have effects similar to those thought to be produced by the thermal regime (Hubbs, 1926; Täning, 1952; Seymour, 1956).

There are exceptions, however, where the change in counts goes contrary to expectations. In certain instances (Schmidt, 1919: 148; Hubbs, 1921: 150; 1924; Schultz, 1927: 420) the counts from one fin only showed an increase associated with warmer temperatures. The other fins manifested the normal negative correlation between number of elements and water temperature.

In spite of laboratory findings that the relationship between meristic structures and developmental temperatures is exceedingly complex, the pattern in natural populations of the same species is usually straightforward: higher temperatures during development normally bring about lower counts (Barlow, 1961*b*).

At first glance the changes in countable characters over the geographic range of *mirabilis* seem to indicate a gradient resulting from direct modification by the environment. Presumably, factors which cause a decrease in the dorsal and anal fin counts conversely bring about an increase in the number of pectoral fin rays.

Geographically, then, the number of median fin rays is negatively correlated with the number of pectoral fin rays. Johnsen (1936: 8-9) reported the same relationship between fins for various populations of *Gobius flavescens* and *Gobius minutus*. These changes could be construed as the result of dissimilar water temperatures or some related factors.

It is more probable, nonetheless, that the cline in meristic characters results primarily from different genotypes, not exclusively from environmental modification. This hypothesis can

be supported by more than one line of evidence.

The gradient of meristic characters in *mirabilis* follows the temperature gradient of the late summer period. The number of rays in the dorsal and anal fins increases from north to south in the Gulf of California, whereas over the same latitude on the Pacific Coast the opposite relation holds, and the counts tend to decrease from north to south. The same reversal of trends between the Gulf and outer coast occurs in the pectoral fin.

The fin indices decrease from north to south on the Pacific Coast, but continue to decrease in the Gulf from south to north. Thus a continuous cline in the meristic characters exists from San Francisco south, on the Pacific Coast, and then north up into the Gulf of California.

It might be argued that the late summer temperature gradient in the Gulf is opposite to that of the outer coast, and that this environmental difference directly accounts for the reversal of the fin-index gradient. This cannot be the case, because the counts are determined while the eggs and larvae develop during late winter through early summer; then the temperature gradients of the Gulf and Pacific Coast are parallel, warmer to the south. If any correlation exists between environmental temperatures and number of countable elements, it is with the gradient of extremely warm temperatures found late in the summer, not those occurring during early development.

This cline, however, might reflect nothing more than the progressive physical separation between populations.

The fin index for *seta* in the upper Gulf of California continues the trend noted in *mirabilis*, that is, for lower indices toward the north in the Gulf. The average value for *seta* there is about 82 as compared to about 95 for adjacent populations of *mirabilis*. The temperature situation that prevails in the habitat of *seta* could be regarded as an extension of the gradient seen in the habitats of *mirabilis* from south to north in the Gulf. The habitat of *seta* is located on the coast in the high intertidal zone among black lava flows, boulders, and streams of seepage water (Barlow, 1961a). Climatically this environment is even more rigorous, and surely experiences higher summer

temperatures than do the nearby sloughs where *mirabilis* occurs.

Returning to the fin indices of *mirabilis*, specimens from the Salton Sea, compared to their parental stock, have much higher counts in their dorsal and anal fins, and in their pectoral fins as well. The differences probably can be attributed to retardation of developmental rate. If the interaction between these fins behaved as expected from observations on the geographical cline, the pectoral fin counts should have decreased while the median fin counts increased. As shown by the fin index, the relationship between median and paired fins, remarkably, is unchanged in these fish.

Fluctuations in the mean number of segmented rays from year to year in a given population are in the same direction for the median fins and the pectoral fins. In other words, the changes in the number of elements in paired and median fins are positively correlated in their response to environmental changes. Colder years induce the formation of more rays in all of these fins.

In each fish, however, the number of pectoral fin rays appears to be inherited independently from the number of median fin rays. In a given year class, the fish with more numerous rays in the median fins have, on the average, the same number of pectoral fin rays as do fish with less median fin rays. Thus the median fin and the pectoral fin elements respond to the environment in the same way, but independently of each other.

From the foregoing evidence it seems reasonable to conclude that the change in relationship between the number of elements in the median fins and in the pectoral fin, the fin index, over the geographic range of *mirabilis* indicates genetic divergence.

Analogous differences between inter- and intra-population variation have been observed in other gobies (Johnsen, 1936: 8–9). In different populations of *Gobius flavescens* and *G. minutus*, the vertebral counts (median fin counts follow vertebral counts) are negatively correlated with pectoral fin counts. In contrast, these meristic characters are positively correlated within a given population; larger fish have more vertebrae and average more pectoral fin rays as well.

Johnsen indiscriminately attributed both kinds of variation to direct modification by the environment.

A further similarity between the results of Johnsen's investigation and the present study lies in the course of divergence of the fin index (calculated from his data). There is a geographic cline in the index which is minimal in the Baltic Sea and increases to the west and then independently south and north in the North Sea, but is maximal to the north.

In *Gillichthys mirabilis*, a genetic cline is also suggested by comparisons of population means of combined fin ray counts. Variation between year classes and a comparison of Salton Sea fish with their parental stock indicate that slower development is correlated with an increase in the total number of fin elements. If the developmental rates within the populations are altered by climatic temperatures, and this is a reasonable assumption, then the combined counts should decrease from north to south. But the combined counts are about the same for all populations, with a few exceptions, and the exceptions are obvious deviants.

One could argue for a cline of combined counts for the seven populations in California. But the counts increase, not decrease, steadily from San Francisco south to San Diego. Such differences from north to south could be attributed to increasingly saline water to the south, or to later spawning seasons to the north. Yet the northernmost habitat, the Alviso salt ponds, is highly saline, and spawning commences at about the same time throughout the range of *mirabilis*.

There seems to be homeostasis of the combined counts in spite of changes in latitude, since over the rest of the range of *mirabilis* the means are about the same from population to population. This suggests genetic compensation, or relatively complete acclimation of developmental rates. The most obvious deviant, the population from just north of San Felipe, is also atypical in body form.

The variance of the countable characters in each population is even more stable than the mean of the characters. It does not appear possible to estimate the respective roles of heredity and environment in producing this constancy.

Even though the means of the counts were found to shift within limits from year class to year class, the variances showed no statistical differences. The environmental changes responsible for the changes in mean counts, most likely temperature, apparently do not influence the variances. This would seem to indicate an intrinsic homeostasis where variability is concerned.

Photoperiod might determine variability. Day length is constant from year to year on the same day at a given location. Since the change in photoperiod over the spawning season increases faster at higher latitudes, one can demonstrate a positive, although perhaps false, correlation between degree of change in day length and variance. Interestingly, estimates of the variances of the different fins in populations of a different but closely related species, *Gillichthys seta* (Barlow, 1961a), fall directly in the midst of the corresponding data (Fig. 10) for *mirabilis*. Somewhat further aside, in two different populations of *seta* the measurements of four body parts, not counts, having different means had the same variances (Barlow, 1961a).

If the variance of each character is largely genetically determined, then the data indicate two different types of clines in *mirabilis*. Based on the variances, there would be a simple linear relationship, north to south, irrespective of whether the populations are situated on the Pacific Coast or on the east or the west coasts of the Gulf of California. The V-like arrangement deduced from the distribution of the means of the counts, the fin indices, and measurements of body parts have already been described and will be summarized below.

The possible relationship between the differential of the photoperiod and the variance cannot be considered as evidence for or against modification or genetic determination. Even though the environment originally may have induced the variance in question, the phenotype easily could have become genetically reinforced.

The kind and pattern of the differences found between the populations of *mirabilis* seem too complex to be accounted for on the assumption that the dissimilarities result chiefly from direct environmental modification. The most obvious part of the explanation is that the divergences

reflect the degree of physical separation between populations. The less the exchange of genetic material, the greater the opportunity for dissimilarities to arise and persist.

If we are to understand why the variation is in a particular direction and not random, then we must first seek correlations between environmental factors and the observed geographic cline. Temperature and illumination are the only obvious parameters suitable to such an inquiry. The only evidence available relates to temperature differences, so illumination will not be treated. This raises the problem, inherent in such an approach, of formulating a self-realizing assumption.

I have already pointed out the crude correlation between the clines of meristic characters reported on and the gradient of temperatures found late in the summer. In another article (Barlow, 1961*b*), I have argued that relatively stable differences in the means of counts between populations probably reflect physiological differences, most likely temperature responses, that are genetically determined. Changes in counts between populations, as suggested by Hubbs (1928), might constitute examples of the well-known Baldwin effect (Baldwin, 1896): phenotypic modification of the counts (resulting from physiological adjustment) becomes genetically augmented and characterizes the population. A similar argument might hold for the differences in variances that apparently are associated with different photoperiods.

Peculiarities of G. mirabilis from the Salton Sea

The Salton Sea is a saline lake situated in the Salton Sink, a northward extension of the Gulf of California basin. According to Carpelan (1958), it has a surface area of about 340 square miles, but a maximum and highly variable depth of only 12 m. The salinity of the water is about 33 ‰, although the Salton Sea is not of marine origin; it has been formed by the inflow and evaporation of Colorado River water. Relative to ocean water, sulfate (2.7 times more concentrated) and calcium (1.9) ions are especially abundant, whereas potassium (0.58) and magnesium (0.75) are appreciably less concentrated. The annual maximum and minimum surface water temperatures are usu-

ally about 36°C and 10°C, respectively. Great daily fluctuation in temperature occurs, especially in shallow water (Barlow, 1958).

The specimens of *mirabilis* from the Salton Sea differ from those on the outer coast in just the ways one would predict for fish whose growth had been drastically retarded. All fin ray counts and the vertebral counts are high (but the relationship between the fin counts is unchanged), supernumerary spiny rays are formed, scalation is incomplete, the head and its related parts are small, the fins are low, and the completion of the interorbital canal is delayed. Anomalies, such as a continuous slit for the anterior and posterior nares, an abbreviated postorbital canal, and flaps on the jaws, are holdovers of conditions usually seen only in postlarvae.

The unusual combination of salts in the water of the Salton Sea probably interferes with the development of the fish. The water temperatures are not to be considered responsible, for they are moderate during that period of early development when the characters are determined. Indeed, the temperatures are comparable to those of habitats along the sea coasts. Other water conditions (oxygen tension, pH, and illumination) also are similar to those encountered by naturally occurring populations. The Salton Sea fish at times are heavily infested with a monogenetic trematode, but so are coastal populations. Besides, many of the characters are determined before hatching and so could not be modified by debilitation caused by parasites (Hubbs, 1927).

The possibility exists, of course, that the *mirabilis* in the Salton Sea have diverged genetically, and that the structural differences are the result of such genetic change. The original stock consisted of merely 500 fish, of which only a fraction could have reproduced successfully. By chance alone, certain alleles must have been lost, others fixed, even if all 500 fish are assumed to have reproduced (Wright, 1951). The population expanded rapidly to a large number of fish, as did later introductions of other species. In a large population, genetic drift would no longer be operative (Wright, 1951). During the 25 years after introduction, selection has been effected, for the most part,

through the rigorous environment and through intraspecific competition.

If the gene pool of the Salton Sea fish has been altered, then the morphological changes might be due to such genetic differences. This cannot be known without rearing experiments. Experiments on the metabolic physiology of the adults suggest slight genetic divergence has taken place (Barlow, 1961c).

My opinion is that the morphological peculiarities of the fish from the Salton Sea can be ascribed primarily to direct modification caused by the chemical composition of the water in which they develop; the same could be said of the San Felipe fish from a saline pool.

Conclusions

The investigation of the species *Gillichthys mirabilis* has revealed a complex situation in which genetic divergence is evidently intertwined with phenotypic plasticity.

Over the range of *mirabilis*, the adaptive norms seem to shift gradually, but with some plateaus. A comparison of fin indices and means of the fin counts indicates the following arrangement: (1) Populations of *mirabilis* are nearly the same genetically on the California coast, though the Salton Sea and San Francisco populations may be somewhat distinct. (2) A genetic cline may exist on the outer coast of Baja California. (3) The fish from the lower region of the Gulf of California are similar to, but slightly different from, those on the outer coast of southern Baja California. (4) The populations found in the northern part of the Gulf have diverged from those of the southern part to a greater degree than can be accounted for, in a consistent manner, by environmentally induced changes.

Investigations of the body form of *mirabilis* support the conclusions based on countable characters. The body form of fish from California is about the same in each of the populations, although local differences exist. Fish from the Gulf of California, as a group, differ from those from California; no adult specimens were available from the outer coast of southern Baja California. Within the Gulf populations, fish in the upper northern region of the Gulf are separable from those in the southern region.

Thus *mirabilis* is seen as one widely ranging species whose geographic subdivisions are consistent with known faunal regions. For example, the fish fauna of San Francisco Bay is isolated from its southern counterpart, and the degree of differentiation of the *mirabilis* population there reflects this separation. The broad transition between faunas along the outer coast of Baja California also seems to be an area of transition for *mirabilis*, though more samples are needed from this region. Likewise, the morphological separation of the *mirabilis* of the Gulf from those of the outer coast is in keeping with the known distribution of this species. Finally, the division of *mirabilis* from the Gulf into northern and southern groups is in harmony with faunistic and oceanographic findings (Hubbs, 1960; Walker, 1960; Roden, 1958).

Subspecific names are not proposed for the geographic variants. Until more collections are available it would only create confusion to name the geographic forms as they are known at present. Even if they were better known, I doubt that subspecific names would be of utility here. None of the evidence suggests that any group, or groups, of populations is evolving into a distinct species. The findings indicate only that in this widely distributed species appreciable differences exist; these are thought to reflect adaptive changes.

SUMMARY

1. *Gillichthys mirabilis* Cooper is found in coastal sloughs from Central California south to near Cabo San Lucas, and then again in the central and northern parts of the Gulf of California. It has been introduced into the Salton Sea.

2. The fish spawn from about January to June and reach maturity within 1 year. The larvae have a brief pelagic phase, during which time the species is distributed to new habitats.

3. The head is shortest in specimens of *mirabilis* from the Salton Sea and most depressed in those from the Gulf of California. The length of the upper jaw and the height of the median fins are greatest in samples from the Gulf and least in those from the Salton Sea. Specimens from the upper Gulf region have the dorsal fins separated more than in *mirabilis* from elsewhere.

4. The scales are larger and the ventral area more scaled in specimens from the Gulf than in those from the outer coast. Scalation is noticeably reduced in fish from the Salton Sea.

5. Trends in means of meristic characters, from north to south along the Pacific Coast, and then from south to north up into the Gulf of California, are as follows: spiny dorsal fin—no change or slight increase; segmented rays of median fins—decrease; pectoral fin—increase; combined fin elements—irregular or no change; fin index (segmented dorsal plus anal rays, divided by pectoral rays, times 100)—decrease; pectoral fin asymmetry—decrease; vertebrae—no change.

6. The variance of the number of elements in each fin is a function of latitude, greater variance being associated with higher latitudes.

7. The means of the counts of the median fin are negatively correlated with the means for pectoral fin rays when the comparison is between the various populations. In successive year classes within a given population, however, changes in the number of rays in the median fins are associated with commensurate changes of the same sign in the counts of the pectoral fin rays. But within each year class there is no correlation between the number of pectoral fin and median fin rays.

8. All meristic characters have higher mean values in specimens from the Salton Sea, but the mean of their fin index accords with the Pacific Coast population from which they were derived. The Salton Sea fish are aberrant in many ways, evidently as a result of living in a marginal environment.

9. The conclusions based on these findings are condensed on the last page of the foregoing article.

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Preliminary Notes on Molluscan Assemblages of the Submarine Banks Around the Izu Islands

TAKASHI OKUTANI¹

IT IS WELL KNOWN that there are several submarine banks along the submerged rise which extends southwestward from the southern tip of Izu Peninsula, central Honshu. Small islands such as Toshima, Niijima, Shikine, and Kozu, with several other islets, lie on this rise. These, together with a few other islands situated farther south, are called the Izu Islands. They are linked by a volcanic system, and there is a considerable number of such banks in the neighborhood. A few papers concerned with hydrographical, bathymetrical, and faunistic characteristics of these submarine banks have been prepared by Suzuki and Sato (1944), Niino (1935, 1952, 1955), and Shirai (1958). On the basis of these works, together with information furnished by the present author, Horikoshi (1957) discussed the topographical peculiarity in relation to the general molluscan fauna on these banks.

Another group of submarine banks is found around the Osumi Islands, south of Kyushu. Presumably their hydrographical and bathymetrical characters are similar to those banks mentioned above, but no information about the molluscan fauna has been available until now.

As a contribution to knowledge about molluscan fauna on the submarine banks and insular shelves around the Izu Islands, this paper deals with the general account of the molluscan assemblages of the area and their faunal similarity to another series of banks near the Osumi Islands in the Kuroshio area. It is based on biological dredge samples collected chiefly by research vessels during 1955-59.

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TOPOGRAPHY OF SUBMARINE BANKS AROUND IZU ISLANDS

The Izu Islands extend from the mouth of Sagami Bay to the south. In the northern group are (Izu-)Oshima, Toshima, Niijima, Shikine, and Kozu. To the south there are Miyake, Mikura, Hachijo, Aogashima, and Torishima as the southern extremity (Figs. 1, 2). The banks are usually isolated from the series of these islands, with depressions deeper than 200 m lying between them. The tops of such types of banks are usually flat and about 80-120 m in depth. They are usually elongate-oval in shape with the axis in a northeast-southwest direction.

The Hyotanse Bank, one of the representatives of this series of banks, located west of Kozu Island, has been described by Niino (1955) as follows: The slopes around the bank are steep and rocks are exposed there; gravels and coarse material cover the broad and flat plain on its top; andesite and basalt, which are very common in the bedrock, are found mingled with liparite gravels together with a number of manganese concretions from the bank; the lithological characters of these rocks are the same as those of the main islands in the Fuji Volcanic Zone. According to gross observation of the present material, the sediments (gravels and shells) are heavily coated by calcareous algae.

The bottom of Zenisu Bank, also studied by Niino (1935), reveals coarse sand and shells,

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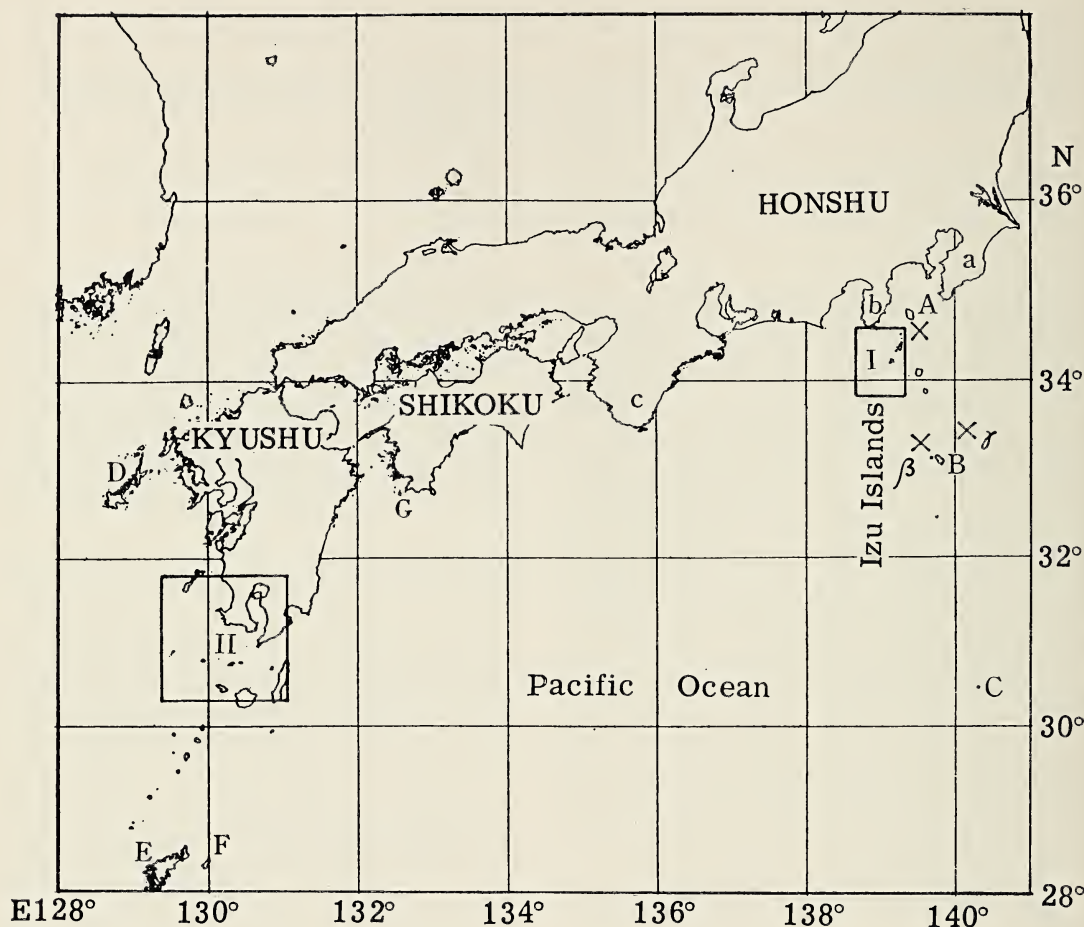


FIG. 1. Index map for the position of submarine banks and other localities. *a*, Boso Peninsula; *b*, Izu Peninsula; *c*, Kii Peninsula. *A*, (Izu-) Oshima Is.; *B*, Hachijo Is.; *C*, Torishima Is.; *D*, Goto Islands; *E*, Amami-Oshima Is.; *F*, Kikaijima Is.; *G*, Okinoshima Is. in the Bungo Straits. *a*, Omurodashii (bank); *β*, Kurose (bank); *γ*, Shinkurose (bank). (See Figs. 2 and 3 for details of areas I and II, respectively.)

and several steep rocks are exposed above the sea surface. At Watarinose Bank, which lies between Kozu Island and Zenisu, the character of the bottom is supposedly generally the same as that at Zenisu. The neighboring waters of those banks are noted as excellent fishing grounds. Kurose and Shinkurose are the southern banks situated around Hachijo Island. The bottom characters of these two are known to be similar to that of Hyotanase. On the other hand, Omurodashii Bank off Izu-Oshima is said to be different from the others in having a sandy mud sediment at its top.

The geographical positions of the submarine banks of Izu Islands under study are referred to in Figures 1 and 2.

OCCURRENCE OF SPECIES BY AREA

1. *Hyotanase Bank*

MATERIAL: Dredged by the R.V. "Soyomaru" on Nov. 20 and 23, 1955, at 7 stations from depths of 118, 135, 140, 145, 148, 153, and 170–230 m.

EARLIER WORKS: Niino (1955) reported 11

species of Pelecypoda and 5 species of Gastropoda. Shirai (1958) reported 5 pelecypods and 5 gastropods.

SPECIES IN THE PRESENT MATERIAL: *Acar congenitum* (Smith); *Mimarcaria aizoi* Sakurai (MS), 137 m; *Striarca fausta* Habe, 137 m; *Samacar pacifica* (Nomura and Zimbo), 137 m; *Barbatia tamikoe* Sakurai (MS), 140 m; *Pseudogrammatodon obliquatus* Yokoyama, var.; *Nipponolimopsis decussata* (A. Ad.), 145 m; *Tucetona shinkurosensis* Hatai, Niino and Kotaka; *Malleus irregularis* (Jousseaume), var., 118 m; *Chlamys mollita* (Rve.), 118 m; *C. lemniscata* (Rve.), 118 m; *C. vesiculosus* (Dkr.); *C. tissotii* (Bernard), 153 m; *Spondylus anacanthus* (Mawe); *Limatula japonica* (A. Ad.); *Lima fujitai* Oyama; *Septifer grayana* (Dkr.); *Cardita nodulosa* (Lamarck), 153 m; *Glans sagamiensis* Kuroda and Habe; *Chama argentata* Kuroda and Habe; *Frigidocardium eos* (Kuroda), 140 m; *Meiocardia tetragona* (Ad. and Rve.); *Emarginula fragilis* Yokoyama, 153 m; *E. teramachii* Habe; *Microgaza* sp. aff. *sericata* Kira, 153 m; *Talopena lifuana* (Fischer), 153 m; *Galeoastrea guttata* (A. Ad.), 153 m; *Tenagodus anguinus* (L.), 140 m; *Serpulorbis medusae* Pilsbry, 140 m; *Apollon hirasei* Kuroda and Habe, 145 m; *Phanozesta semitorta* Kuroda and Habe, 135 m; *Latiaxis pagodus* (A. Ad.), 137 m; *Bursa ranelloides* (Rve.), var., 135 m; *Mitrella* sp. cf. *lischkei* (Smith); *Conus gratapy* Pilsbry, 170 m; *Conus* sp., 153 m.

OTHER SPECIES REPORTED BY NIINO: *Tucetona hanzawai* (Nomura and Zimbo); *Limopsis tajimae* (Yokoyama); *Hawaiarca uwaensis* (Yokoyama); *Plicatula muricata* (Sowerby); *Trichomusculus coralliophaga* (Gmelin); *Lima basilanica* (Ad. and Rve.), 260 m; *Ctenoides annulata* (Lamarck), 260 m; *Pecten albicans* (Schröter); *Lucinoma spectabilis* (Yokoyama); *Perotrochus beyrichii* (Hilgendorf), 134, 160, 128 m.

MOLLUSCS REPORTED ONLY BY SHIRAI: *Limopsis obliqua* A. Ad., 250 m; *Septifer excisus* (Wiegmann), 104 m (this may be *S. grayana*); *Fragum loochooanum* Kira, 250 m (this may be *Glans sagamiensis*); *Galeoastrea millegranosa* Habe, 260 m (this may be *G. guttata*); *Siliquaria cumingii* Mörch, 260 m (this may be *Tenagodus anguinus*).

2. Zenisu Bank

MATERIAL: Dredged by the R.V. "Soyomaru" on Nov. 20, 1955, at 2 stations from depths of 85 and 170 m.

EARLIER WORKS: Niino (1935) reported on the bottom character only.

SPECIES IN THE THE PRESENT MATERIAL: *Acar congenitum* (Smith); *Hawaiarca uwaensis* (Yokoyama), 170 m; *Pseudogrammatodon obliquatus* (Yokoyama); *Pectunculina cernata* (A. Ad.); *Limopsis cumingii* A. Ad.; *Tucetona shinkurosensis* Hatai, Niino and Kotaka, 170 m; *Glycymeris rotunda* (Dkr.); *Polynemamusium intuscostatum* (Yokoyama); *Chlamys vesiculosus* Dkr.; *C. tissotii* (Bernardi); *C. lemniscata* (Rve.); *Plicatula muricata* (Sowerby); *Spondylus anacanthus* (Mawe); *Pecten albicans* (Schröter); *Lima zushiensis* (Yokoyama); *Volsella* sp.; *Pycnodonta musashiana* (Yokoyama); *Meiocardia tetragona* (Ad. and Rve.); *Frigidocardium eos* (Kuroda); *Poromya flexuosa* (Yo-

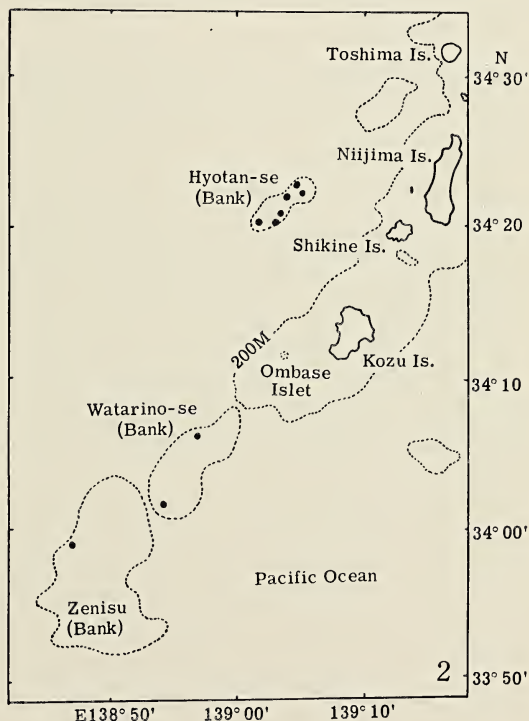


FIG. 2. Detail for I in Fig. 1. Dots indicate the biological stations for the R.V. "Soyomaru" in Nov., 1955.

koyama); *Verticordia japonica* A. Ad.; *Emarginula incisura* A. Ad.; *Bursa ranelloides* (Rve.), var.; *Distorsio* sp.

3. Watarinose Bank

MATERIAL: Dredged by the R.V. "Soyo-maru" on Nov. 20, 1955, at 2 stations from depths of 80–100 m and 140–220 m.

EARLIER WORKS: None.

SPECIES IN THE PRESENT MATERIAL: *Acar congenitum* (Smith); *Barbatia tamikoae* Sakurai (MS); *Samacar pacifica* (Nomura and Zimbo); *Tucetona shinkurosensis* Hatai, Niino and Kotaka; *Malleus irregularis* (Jousseume), var.; *Chlamys mollita* (Rve.); *C. lemniscata* (Rve.); *Lima fujitai* Oyama; *Astraea okamotoi* Kuroda and Habe; *Galeoastrea guttata* (A. Ad.); *Casmaria cervica* (Sowerby)?; *Tenagodus anguinus* (L.); *Clavus* sp. aff. *rufovaricosa* Kuroda (MS).

4. Toshimatai Bank and Niijima Nishitai Bank (Toramaguri)

MATERIAL: None is available for the present study except *Glans sagamiensis* Kuroda and Habe and *Conus kinoshitai* Kuroda from Niijima-Nishitai.

EARLIER WORKS: Niino (1955) reported 19 pelecypods and 4 gastropods from Toramaguri and a single gastropod from Toshimatai. Shirai (1958) reported 9 bivalves and 4 univalves from Niijima-Nishitai Bank.

SPECIES REPORTED BY NIINO AND SHIRAI: Toshimatai Bank—*Tucetona shinkurosensis* Hatai, Niino and Kotaka; *Hiatella arctica orientalis* Yokoyama; *Perotrochus beyrichii* (Hilgendorf), 88 m.

Niijima-Nishitai Bank—*Barbatia plicata* (Dillwyn) (probably *A. congenitum*), 120 m; *Tucetona shinkurosensis* Hatai, Niino and Kotaka, 104 m; *Chlamys pelseeneri* Dautzenberg and Bavay, 120 m; *C. vesiculosus* Dkr., 78 m; *Lima zushiensis* Yokoyama, 73 m; *Lima fujitai* Oyama, 104 m; *Limatula japonica* A. Ad., 104 m; *Crassatellites oblongatus* (Yokoyama), 120 m; *Venus toreuma* Gould, 78 m; *Aloides venusta* (Gould), 120 m; *Perotrochus beyrichii* (Hilgendorf), 104, 120 m; *Emarginula fragilis* Yo-

koyama, 104 m; *E. sp.*, 104 m; *Puncturella fastigiata* A. Ad., 78 m; *Trivirostra oryza* (Lamarck), 88 m.

5. Ombase Islet (near Kozu Island)

MATERIAL: A part of the specimens dredged by the R.V. "Tonan-maru" at depths of 32, 55, 60, and 100 m. These were examined by courtesy of Mr. Kurata.

EARLIER WORKS: Igarashi and others (1956) reported on the bottom character and upon piscifuna from the viewpoint of fishing ground investigation.

SPECIES IN THE PRESENT MATERIAL: *Samacar pacifica* (Nomura and Zimbo), 60 m; *Barbatia* sp.; *Tucetona shinkurosensis* Hatai, Niino and Kotaka, 32 m; *Glycymeris amamiensis* Kuroda, 32 m; *Venus toreuma* Gould; *Galeoastrea guttata* (A. Ad.), 55, 100 m.

6. Kurose and Shinkurose

MATERIAL: Collected from Kurose Bank at a depth of ca. 200 m by *Corallium* fishing net of the R.V. "Tonan-maru." Examined by courtesy of Mr. Kurata.

EARLIER WORKS: Niino (1952) surveyed around Shinkurose Bank and reported 13 gastropods, 20 pelecypods including 3 new forms, and 1 scaphopod.

SPECIES IN THE PRESENT MATERIAL: Kurose Bank—*Acar congenitum* (Smith); *Arca mauia takii* Hatai, Niino and Kotaka; *Barbatia* sp.; *Samacar pacifica* (Nomura and Zimbo); *Lima fujitai* Oyama; *L. quantoensis* Yokoyama; *Crassatellites oblongata* Yokoyama; *Perotrochus beyrichii* (Hilgendorf); *Emarginula* sp.; *Tenagodus anguinus* (L.); *Bursa ranelloides* (Rve.) var.; *Chicoreus laciniatus* (Sowerby); *Conus* sp.

Shinkurose (Niino)—*Arca* sp., 290 m; *Nipponolimopsis nipponica* (Yokoyama), 290 m; *Tucetona hanzawai* (Nomura and Zimbo), 280 m; *Tucetona shinkurosensis* Hatai, Niino and Kotaka, 290 m; *Venericardia ryukyuensis* Nomura and Zimbo, 290 m; *Vasticardium* sp., 280 m; *Chione chlorotica*, 280 m; *Cadulus* sp., 290 m; *Collisella heroldi* (Dkr.), 290 m (a littoral species, may be carried down to the deep by some means); *Margarites cinereus* (Couthouy), 290

m; *Pseudoliotia micans* (A. Ad.), 290 m; *Clathrofenella reticulata* (A. Ad.), 290 m; *Mucronalia subulata* (A. Ad.), 290 m; *Tonna luteostoma* Küster, 280 m; *Coralliophaga eugeniae* (Bernard), 280 m; *Bursa bufonia* (Gmelin), 280 m; *Conus* sp. (identified as *C. ione* by an illustration in Niino's paper).

7. Insular Shelf around Hachijo Island

MATERIAL: None is available here.

EARLIER WORKS: Niino (1952) reported 13 pelecypods and 3 gastropods from depths of 115 and 200 m.

SPECIES REPORTED BY NIINO: *Barbatia hachijojimensis* Hatai, Niino and Kotaka, 115, 200 m; *Arca mauii takii* Hatai, Niino and Kotaka, 200 m; *Tucetona* sp., 200 m; *Spondylus cruentus* Lischke (*S. anacanthus*?), 115 m; *Spondylus* sp.; *Lima lima* L. 115, 200 m; *Pycnodonta musashiana* (Yokoyama), 200 m; *Pseudochama* sp., 200 m; *Vasticardium arenicolum* (Rve.); *Meretrix* sp., 115 m; *Callista pilsbryi* Habe, 200 m; *Venus* sp., 200 m; *Phalium* sp., 115 m; *Ocenebra adunca* (Sowerby), 115 m; *Conus* sp., 115 m.

8. Insular Shelf around Torishima Island

MATERIAL: Part of specimens collected by test fishing for *Corallium* operated at a depth of 150–250 m. The material was examined by courtesy of Mr. Kurata.

EARLIER WORKS: None.

SPECIES IN THE PRESENT MATERIAL: *Spondylus anacanthus* (Mawe); *Pycnodonta musashiana* (Yokoyama); *Plicatula muricata* (Sowerby); *Notolimea* sp. cf. *tosana* Oyama; *Chama argentata* Kuroda and Habe; *Tenagodus anguinus* (L.); *Talopena lifuana* (Pilsbry); *Cantarus* sp.

SIMILAR MOLLUSCAN FAUNA FROM SOME BANKS SOUTHWEST OF KYUSHU

On the Pacific Ocean side of Japan, groups of submarine banks other than those mentioned above are scattered throughout the southwestern waters off Kyushu (Figs. 1, 3). These also are situated on the submarine rise of the volcanic

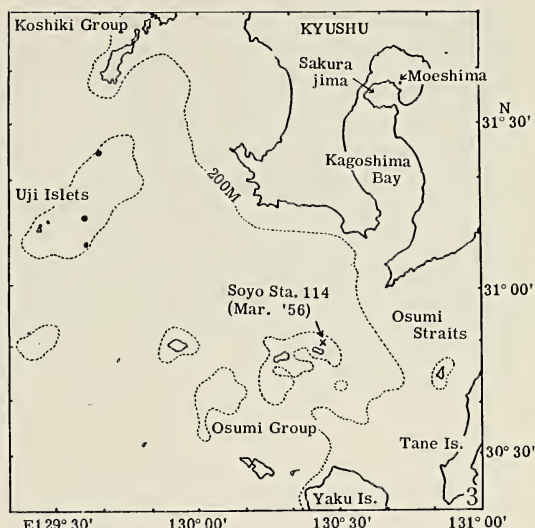


FIG. 3. Detail for II in Fig. 1. Dots indicate the biological stations for the R.V. "Soyo-maru" in Feb., 1959.

canic system on which the Osumi Group lies; this situation is quite similar to that of the Izu Banks. Hereafter, this second series of banks is tentatively called the Osumi Banks. The tops of these banks are usually at about 100 m, and they are isolated from the neighboring islands by depressions of about 200 m in depth. Their general features are similar to the Izu Banks in that they have submarine sediments of coarse sand and gravel which are coated by calcareous algae. Some rocks exposed at the sea surface are also found (e.g., the Uji Islets).

Oceanographically, the two series of banks are decidedly exposed to similar conditions with respect to the Kuroshio Current, for the usual main axis of the current passes through the Osumi Straits as well as across the Izu Submarine Ridge.

The occurrence of molluscan species revealed by the present survey is as follows:

9. Off Takeshima Island

At a depth of 210 m; dredged by the R.V. "Soyo-maru" on Mar. 5, 1956; sta. 114: 30° 50' N, 130° 28' E.

Arca mauii takii Hatai, Niino and Kotaka;

Glycymeris amamiensis Kuroda; *Chlamys molita* (Rve.); *C. vesiculosus* (Dkr.), var.; *C. tissotii* (Bernardi); *Lima tomlini* Prasad; *Ctenoides japonicus* (Dkr.); *Plicatula muricata* Sowerby; *Septifer grayanus* (Dkr.); *Glans kyu-shuensis*, n. sp.; *Chama argentata* Kuroda and Habe; *Frigidocardium eos* (Kuroda); *Vastocardium* sp.; *Venus toreuma* (Gould); *Pitar* sp.; *Bursa* sp.; *Galeoastrea millegranosa* Habe; *G. tayloriana* (Smith); *Ceratostoma vespertilis* Kira; *Chicoreus laciniatus* (Sowerby)?; *Polynices* sp.; *Conus* sp.

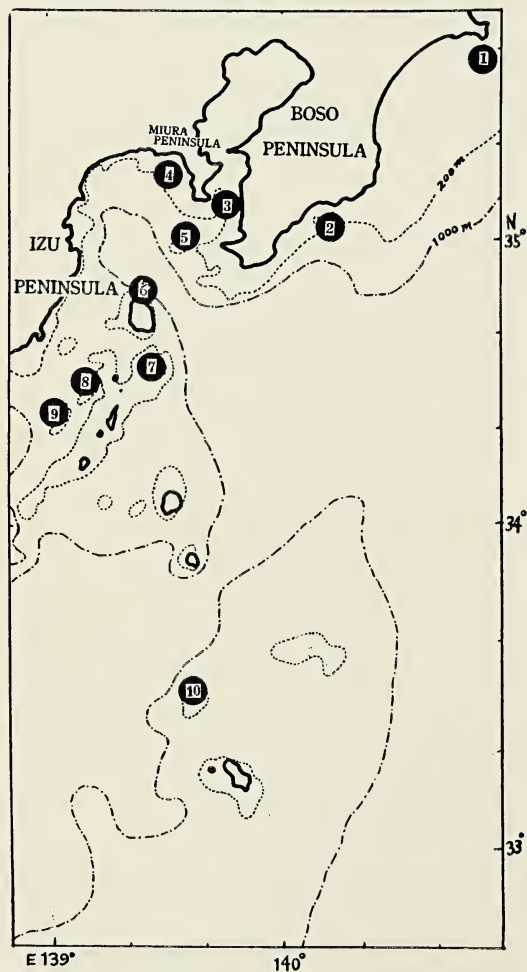


FIG. 4. Distribution of *Perotrochus beyrichii* (Hilgendorf). (See section 12 for numerals on dots.)

10. Uji Islets

At 3 stations from depths of 126–140 m; dredged by the R.V. "Soyo-maru" on Feb. 8, 1959.

Acar congenitum (Smith), 126 m; *Striarca fausta* Habe, 126 m; *Samacar pacifica* (Nomura and Zimbo), 126 m; *Mimarcaria aizoi* Sakurai (MS), 126 m; *Hawaiarca uwaensis* (Yokoyama), 126 m; *Spondylus anacanthus* (Mawe), 126 m; *Chlamys lemniscata* (Rve.), 140 m; *Malleus irregularis* (Jousseume), 126 m; *Chama argentata* Kuroda and Habe, 126 m; *Atrina penna* Habe, 140 m; *Penicillus giganteus* (Sowerby), 126 m; *Perotrochus salmiana* (Rolle), 126 m; *Serpulorbis medusae* Pilsbry, 126 m; *Emarginula* sp.; *Malluvium otobimeae* (Habe), 140 m; *Bursa ranelloides* (Rve.), var., 126, 140 m; *Semicassis* sp., 140 m.

11. Insular Shelf around Goto Islands

Sakurai (1959, and personal communication) reported the following species which have been collected by *Corallium* fishing nets operated off the Goto Islands; depths of operation may be about 100–200 m.

Mimarcaria aizoi Sakurai (MS); *Barbatia tamikoeae* Sakurai (MS); *Acar congenitum* (Smith); *Striarca fausta* Habe; *S. soyoae* Habe; *Chlamys lemniscata* (Rve.); *Dymia argentata* Habe; *Samacar pacifica* (Nomura and Zimbo); *Chama argentata* Kuroda and Habe; *Perotrochus hirasei* Pilsbry.

TYPICAL SPECIES OR SPECIES-GROUPS FOR BANKS-ASSOCIATED MOLLUSCA

Because the present data are not based on quantitative samplings, it is not possible to discuss the matter from a quantitative point of view. However, several species-groups may be indicated as endemic ones (or semiendemic) for submarine banks or insular shelves, because of their frequency or abundance in occurrence.

12. *Perotrochus beyrichii* (Hilgendorf)

Fig. 5

It is well known that this "living fossil" occurs on the lower shelf around Sagami Bay. The

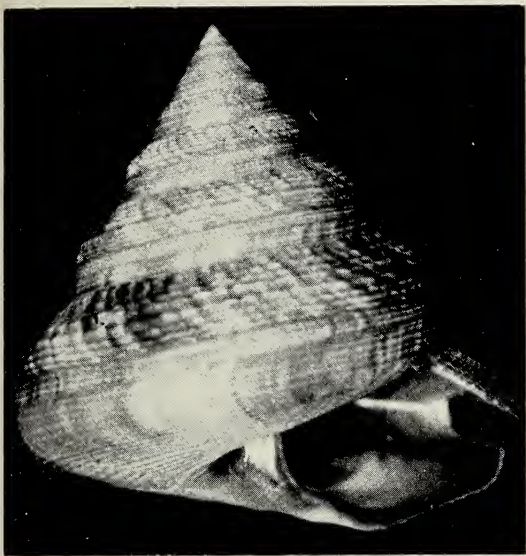


FIG. 5. *Perotrochus beyrichii* (Hilgendorf) from Kurose, ca. 200 m, 72.7 mm $\times$ 70.0 mm (Mr. Kurata coll.).

known localities of the species are as follows (numbers for records refer to those of localities shown in Fig. 4):

- 1) Off Iioka, Pacific side of Boso Peninsula; dead shells collected by commercial trawlers (Sakurai, 1954).
- 2) Off Hachiman-Saki ("Soyo" sta. 40a; July 4, 1956; 35° 04.7' N, 140° 21.5' E), 250 m in depth; a fragment only.
- 3) West coast of Boso Peninsula, off Katsuyama and Tomiura, about 200–300 m in depth (Wada, 1954).
- 4) Sagami Bay, west coast of Miura Peninsula. Type locality is off Misaki. Also collected by the H. M. "The Emperor" near Hayama.
- 5) Okinoyama, a small bank located near the southwestern tip of Boso Peninsula.
- 6) Senzu, northwestern coast of Oshima Island; dead shell with hermit crab, collected by Mr. Kurata.
- 7) Around Omurodashi Bank (Shirai, 1958).
- 8) Hyotanse, 128, 134, 160 m (Niino, 1955).
- 9) Niijima-Nishitai, 104, 120 m; and Toshimatai, 88 m (Niino, 1955, and Shirai, 1958).
- 10) Kurose, collected by Mr. Kurata.

As is shown above, this pleurotomariid gastropod is characteristically distributed on the lower shelf and submarine banks around the area. Other species of *Perotrochus*, as ecological equivalents, are also found in similar habitats in other districts; *Perotrochus hirasei* Pilsbry is known to be distributed around the Pacific coast of Kii Peninsula and Tosa Bay, and as an inhabitant of the continental shelf around the main Japanese islands. According to Mr. Teramachi (personal communication), *P. hirasei* has been collected by him from depths of 60 fathoms (ranging 20–180 fathoms) in such localities.

- 1) Okezoko Deep located south of Okinoshima Islet in Bungo Straits. This is collected from thanatocoenose, mainly of *Glycymeris rotunda*, with *Siphonalia filosa*, etc.
- 2) Off Urado in Tosa Bay, 70–80 fathoms, sometimes with *Erronea hirasei*, *Chicoreus dilectus*, and some other common shelf dwellers.
- 3) Off Tanabe, southwestern coast of Kii Peninsula.
- 4) Somewhere in Hyuga-Nada, eastern waters off Kyushu.

Recently, Kuroda and Habe (1953) have shown that this species is also distributed in the



FIG. 6. *Perotrochus salmiana* (Rolle) from Uji Islet, 126 m, 65.0 mm $\times$ 62.7 mm.



FIG. 7. Distribution of three species of Japanese *Perotrochus*. Dots, *P. beyrichii*; horizontal lines, *P. hirasei*; cross lines, *P. salmiana*.

western waters off Kyushu and around the Goto Islands, where some banks-associated assemblages are found (Sakurai, 1959, and cf 11). *Perotrochus salmiana* (Rolle) (Fig. 6) is also known from waters off Kii and Tosa provinces. In the present survey, a new locality for this rare species was discovered from the Uji Islets ("Soyo" sta. 72a, Feb. 8, 1959, $31^{\circ} 24.7' N$, $129^{\circ} 37.6' E$, 126 m), in company with the similar banks-associated fauna (cf 10). The smallness of the specimen in the present material may coincide with the fact pointed out by Parker and Curray (1956: 2436), "... most of these bank forms were considerably smaller, although they appeared to be mature specimens. ..."

13. *Galeoastrea guttata* (A. Adams)
Fig. 8

According to Habe (1958), this fascinating species is distributed around Boso Peninsula and Sagami Bay. As is shown in the map (Fig. 20a), this species is characteristically distributed on the banks around the Izu Islands, i.e., Hyotanse, Ombase Islet, and Okinoyama. It is very rare from the insular shelf, despite the fact that there is an example from the Izu Penin-

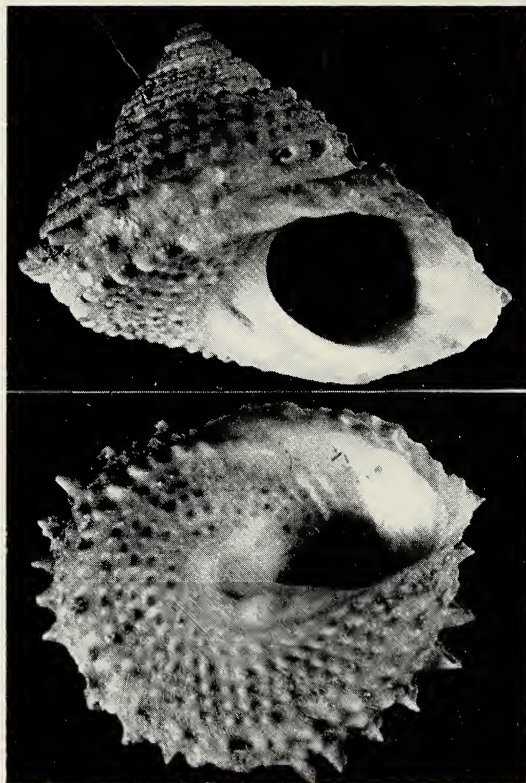


FIG. 8. *Galeoastrea guttata* (A. Adams) from Hyotanse, 153 m, 22.2 mm $\times$ 30.3 mm.

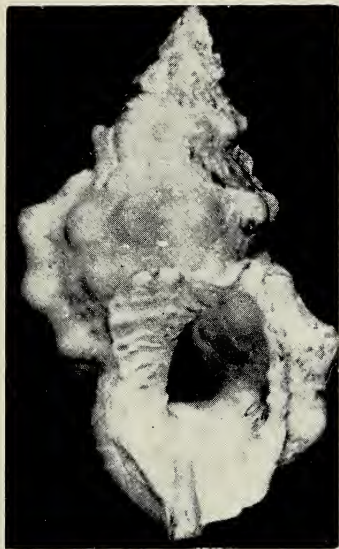


FIG. 9. *Bursa ranelloides* (Reeve) var. from Uji Islet, 140 m, 48.6 mm × 30.3 mm.

sula coast off Iro-Zaki ("Soyo" sta. 42, Apr. 2, 1958, 34° 34.2' N, 138° 50.7' E, 80 m). No record from Boso Peninsula is available for the present study. A possible ecological equivalent,

G. millegranosa Habe, is distributed on the Osumi Banks as well as in its adjacent waters, where *G. guttata* is not found. It is also interesting to note that one of the related species, *Astraea caelata* Gmelin, is indicated by Parker and Curray (1956) as a typical banks-associated mollusca from calcareous banks on the continental shelf off Texas, U.S.A.

14. *Bursa ranelloides* (Reeve) var.

Fig. 9

A rather small form of the species is widely distributed on the banks mentioned above. It has been collected from Hyotanse, 135 m; Zenisu; Kurose, 200 m; off Takeshima, 210 m, and the Uji Islets, 126 m.

15. *Small Arcid Pelecypods*

Figs. 10, 11

On the submarine banks under study, some small species of Arcidae are abundant and are found together with other members of the group. The occurrence of species in the present material is as follows:

	IZU BANKS			OSUMI BANKS (KYUSHU)		
	Hyotanse	Zenisu	Kurose	Goto	Uji	Sta. 114
<i>Acar congenitum</i> (Smith).....	+	+	+	+	+	—
<i>Arca mauia takii</i> Hatai, Niino, Kotaka....	—	—	+	—	—	+
<i>Mimarcaria aizoi</i> Sakurai (MS).....	+	—	—	+	+	—
<i>Hawaiarca uwaensis</i> (Yokoyama).....	+	+	—	+	+	—
<i>Samacarc pacifica</i> (Nomura, Zimbo).....	+	—?	+	+	+	—
<i>Striarca fausta</i> Habe.....	+	—	—	+	+	—

16. *Small Pectinid Pelecypods*

Figs. 12–14

Chlamys vesiculosus (Dkr.) is known to be very abundant on the continental shelf bordering southwestern Japan. Being a sandy bottom dweller, it is also distributed on the banks of the northern group at a depth of 32–118 m. A related species, *C. tissotii* (Bernardi), often occurs in the same localities. They are not found

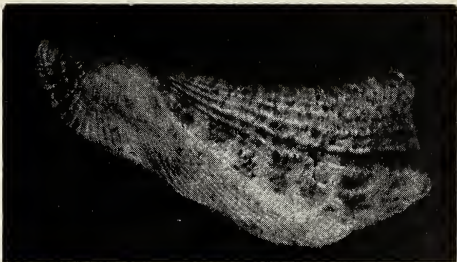


FIG. 10. *Arca mauia takii* Hatai, Niino, and Kotaka from Kurose ca. 200 m, 28.0 mm × 15.0 mm (Mr. Kurata coll.).

on the southern half of Izu Banks but are distributed on the Osumi Banks. *C. lemniscata* (Rve.) is similar in its distribution to the pre-

ceding two species; it occurs rather oftener than *C. mollita* (Rve.) does on the banks under study.

	IZU BANKS			OSUMI BANKS	
	Hyotanse	Zenisu	Kurose	Uji	Sta. 114
<i>Chlamys vesiculosus</i> (Dkr.).....	+	+	—	+	+
<i>C. tissotii</i> (Bernardi).....	+	+	—	+	+
<i>C. lemniscata</i> (Rve.).....	+	+	—	+	—
<i>C. mollita</i> (Rve.).....	+	—	—	+	+

17. *Tucetona hanzawai* (Nomura and Zimbo);
T. shinkurosensis Hatai, Niino, Kotaka
Figs. 15, 16

These small glycymerid species occur on the banks under study. As the former, *T. hanzawai*, originally described from a fossil bed of Ryukyu (Riu Kiu) Limestone, was recorded from Hyotanse and Shinkurose (Niino, 1952, 1955). Hatai, Niino, and Kotaka (in Niino, 1952: 106) stated that "the occurrence of this species

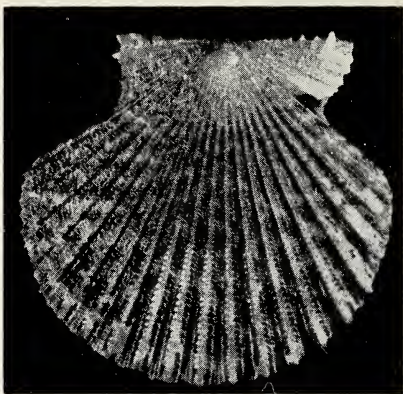


FIG. 12. *Chlamys tissotii* (Bernardi) from Hyotanse, 140 m, 12.6 mm × 13.4 mm.

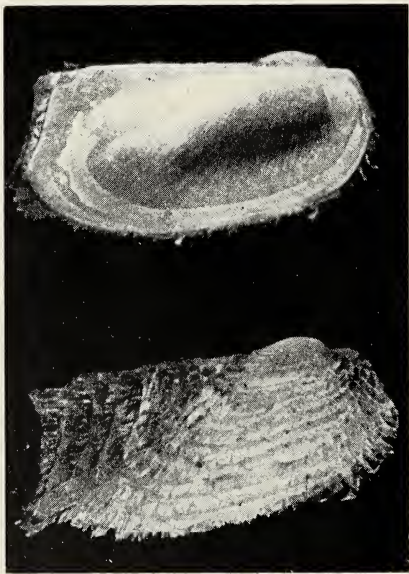


FIG. 11. *Samacar pacifica* (Nomura and Zimbo) from off Miyake Island, 170 m, 12.5 mm × 6.5 mm.

in the marine fauna of the environs of Hachijo Island is interesting, because it may suggest the occurrence of a submerged (geological) formation corresponding in age to the Ryukyu Limestone." The latter species has been found from Shinkurose (the type locality), Hyotanse, Zenisu, Watarinose, Nijjima-Nishitai, Toshimatai, as well as Ombase Islet (Fig. 20*b*).

According to Hatai, Niino, and Kotaka (in Niino, 1952), *T. shinkurosensis* (loc. cit. p. 109, figs. 11, 12) is distinguished from *T. hanzawai* (Nomura and Zimbo, 1934, p. 152(44), pl. 5(1), figs. 3*a*, *b*: as *Glycymeris*) by the following points: The shell of *T. shinkurosensis* is longer than high, while that of *T. hanzawai* is higher than long; the radial ribs of the former are broad, flat, low, and are 27 in number, while

there are 25 rounded ribs in the latter species; the interspaces of *shinkurosensis* ribs are much narrower than the ribs, while the interspaces of the latter species are nearly equal to the ribs; the hinge teeth of the former are 5 in the anterior half and 6 in the posterior half, instead of 8 and 9 on the anterior and posterior half of the hinge plate of the latter species.

In the present survey, 40 odd valves from Izu Banks were examined. The size ranges of the material were 7.7–17.4 mm in length and

7.6–18.1 mm in height. Of these specimens, no valve was found which had rib interspaces as wide as the ribs themselves, despite the fact that meristic characters vary with individuals, i. e., height/length, ranges 0.915–1.090; number of radial ribs, 24–33; anterior hinge teeth, 5–10; posterior teeth, 7–11. On these evidences, all of the specimens are identified as *T. shinkurosensis*.

The measurements of two odd valves of topotypes of *T. hanzawai* are:

	HEIGHT	HEIGHT/LENGTH	RADIAL RIBS	TEETH	
				Ant.	Post.
No. 1 (left valve)	11.1 mm	1.057	29	7	7
No. 2 (right valve)	12.0 mm	1.190	25	8	7

The interspaces of radial ribs are estimated to be about half as wide as the ribs. In comparison with specimens of two species of similar size, *T. hanzawai* is provided with more distinguishing features than are pointed out in the foregoing lines: it has a more prominent umbo, a deeper shell, and less angular shoulders, thus a *Vasicardium*-like appearance, partly because of its shell which is longer than it is high. Nevertheless, the morphological similarity of these two requires further biometrical study in the future.

GEOGRAPHICAL DIFFERENCES AND VERTICAL LIMITS OF TYPICAL BANKS-ASSOCIATED ASSEMBLAGES

Since the present material was obtained with different kinds of gear from a limited number of stations, a conclusive quantitative analysis can not be made at present. However, the abundance or probable dominance of the several

18. *Chama argentata* Kuroda and Habe
Fig. 17

This is found on many banks and insular shelves under study. It was collected from the Niijima-Nishitai Banks, the insular shelf of Torishima, the Uji Islets, insular shelves of Takeshima (Sta. 114), and the Goto Islands (Fig. 20c).

Other species than those enumerated above, *Spondylus anacanthus* (Mawe), *Plicatula muricata* (Sowerby), and *Lima fujitai* Oyama (Figs. 18, 19, and 20d), are usually found abundantly in the area. The occurrence of two or three of them may be a remarkable faunal characteristic of the banks.

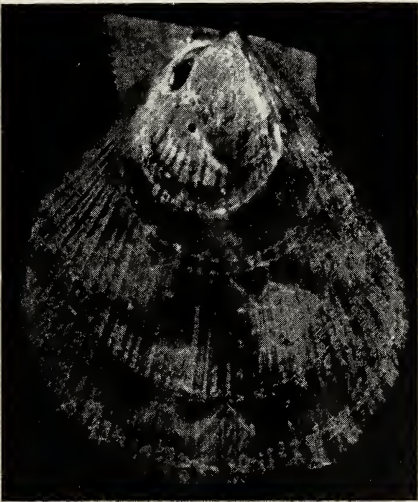


FIG. 13. *Chlamys lemniscata* (Reeve) from Uji Islet, 126 m, 22.0 mm × 20.0 mm.

species might be estimated. If in the future these areas are more thoroughly surveyed by quantitative methods, the faunistic differences or peculiarities will be more clearly demonstrated. For the same reason, present data are presumed to be insufficient for the following discussion and a supplemental report is to be expected.

Geographical Differences of the Assemblages

Within the Izu Banks, local differences in the assemblage are scarcely observed. The typical species-groups found in the area are roughly subtropical or warm-temperate forms from the lower part of the continental shelf bordering the main Japanese islands. On the other hand, probably because of the differences in latitude, a slight difference exists between the faunas of the northern half and those of the southern half of the Izu Banks.

Geographically, the Izu Islands and the Osumi Group are distant from each other. Similar patches of banks are not found between the Izu Banks and the Osumi Banks. Therefore, the continuity or discontinuity of the fauna has not yet been studied. However, many species are found in both areas: *Arca mauii takii* Hatai, Niino, and Kotaka; *Acar congenitum* (Smith); *Samacar pacifica* (Nomura and Zimbo); *Hawaiarca uwaensis* (Yokoyama); *Mimarcaria aizoi* Sakurai (MS); *Striarca fausta*

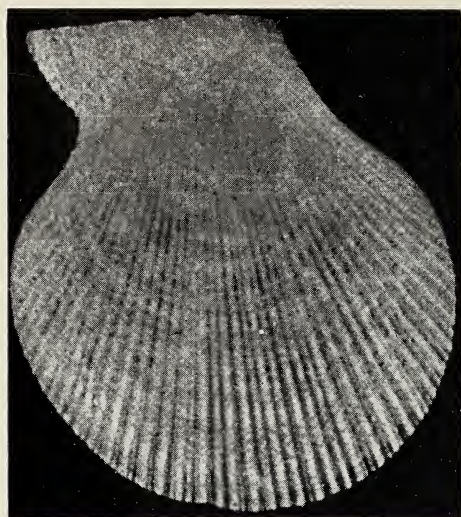


FIG. 14. *Chlamys mollita* (Reeve) from Hyotanase, 118 m, 18.5 mm $\times$ 17.0 mm.

Habe; *Chlamys vesiculosus* (Dkr.); *C. tissotii* (Bernardi); *C. lemniscata* (Rve.); *C. mollita* (Rve.); *Spondylus anacanthus* (Mawe); *Plicatula muricata* (Sowerby); *Frigidocardium eos* (Kuroda); *Chama argentata* Kuroda and Habe; *Tenagodus anguinus* (L.); *Bursa ranelloides* (Rve.), var.; and *Conus* sp.

Of the species that are not common to the two areas, some forms are apparently ecological equivalents of banks-associated forms. Several examples are shown here:

IZU ISLANDS AREA	OSUMI STRAITS AREA
<i>Perotrochus beyrichii</i> (Hilgendorf) <i>Galeoastrea guttata</i> (A. Ad.)	<i>P. salmiana</i> (Rolle) <i>G. millegranosa</i> Habe or <i>G. tayloriana</i> (Smith)
<i>Tucetona shinkurosensis</i> Hatai, Niino, and Kotaka <i>Lima fujitai</i> Oyama <i>Glans sagamiensis</i> Kuroda and Habe	<i>L. tomlini</i> Prasad? <i>G. kyushensis</i> , sp. nov.

Possible Vertical Limits of the Banks-Associated Fauna

The distribution of the benthic mollusca is governed much more forcefully by the substratum of the depths than by other environmental factors. At equal depths in similar latitudinal position, or under the same ocean

climate, the differences in representation are due to such bottom factors as mud, sand, gravel, and rock. The banks-associated molluscan assemblages shows mainly hard-bottom facies mingling with some sandy bottom dwellers of the depths. This is closely associated with the insular shelf fauna, since the surrounding areas of almost all the small islands in the region are

almost entirely rocky. On the other hand, this is not always similar to the shelf fauna of the main islands because the shelf bordering the main islands does not always present a hard bottom. For instance, a molluscan assemblage from the soft bottom within Sagami Bay at a similar depth ("Soyo" sta. T26, Nov. 15, 1958, $35^{\circ} 15.4' N$, $139^{\circ} 27.9' E$, 102 m) is made up of: *Glycymeris rotunda* (Dkr.); *Delectopecten macrocheilicola* Habe (believed to be found attached to the carapace of the giant spider crab, but recently recovered as free living individuals); *Venus faveolatus* Sowerby; *Onustus exutus* (Reeve); *Granulifusus niponicus* (Smith). Moreover, collections from a certain area in Sagami Bay sometimes contain species similar to those from the banks under study (cf 12 and 13), while a different assemblage is found from another hard bottom in the Bay at the same level. Therefore, the most remarkable character of a banks-associated assemblage is the constant occurrence and constant dominance of the typical species of the area.

The typical banks-associated assemblage appears at depths ranging from 32 m as the shallowest to 290 m as the deepest, centering around 100–250 m. In waters shallower than this, a certain upper-shelf assemblage is observed, which is frequently collected by a lobster-net or in *Gelinidium* collecting. Examples of hard-bottom dwellers in the shallower zones of the Oshima Islands are: *Turbo cornutus* (Solander); *Fusinus nicobaricus* (Lamarck); *Fasciolaria glabra* (Dkr.); *F. trapezium audouini* (Jonus),

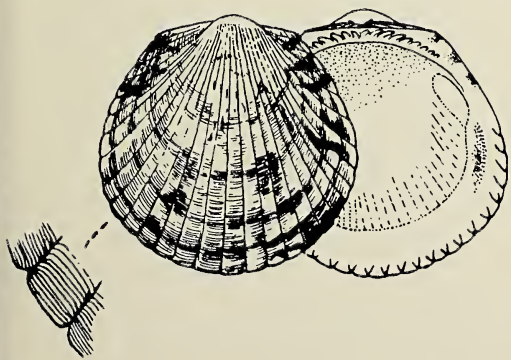


FIG. 15. *Tucetona shinkurosensis* Hatai, Niino, and Kotaka from Niijima-Nishitai, 14 mm in height.

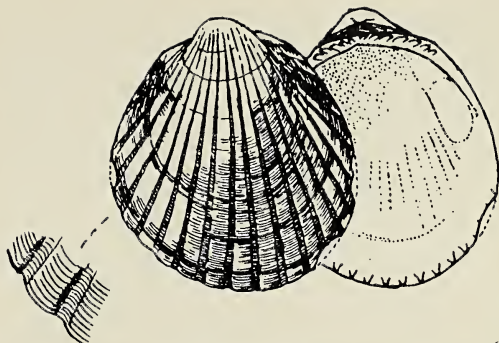


FIG. 16. *Tucetona hanzawai* (Nomura and Zimbo) from Kikaijima (fossil).

etc. The sandy bottom facies of the upper shelf in Okada, Oshima Island, is reported by the dominance of the following species: *Terebra nebulosa* Sowerby; *Conus tessulatus* Born; *Chlamys vesiculosus* (Dkr.); *Callista pilsbryi* Habe; *Dosinia iwakawai* Oyama and Habe; *Antigona lamellaris* Schumacher; *Sunetta concinna* (Dkr.), var.; *Paphia amabilis* (Philippi).

Judging from these observations, the ecotone between a shallow insular shelf fauna and a lower insular shelf fauna, which is almost equivalent to banks-associated fauna, is presumably at a depth of 50 m or so. The deeper limit may be about 300 m. For example, at a station near Okinoyama, about 300 m deep, the following species were collected from a gravel bottom ("Soyo" sta. T20'C, Aug. 11, 1958, $34^{\circ} 59.0' N$, $139^{\circ} 32.3' E$) despite the fact that the similar banks-associated assemblage is observed on the upper part of this bank: *Chlamys* sp. aff. *mollita* (Rve.); *Delectopecten macrocheilicola* Habe; *Keenaea sakuraii* Habe; *Pandora* sp.; *Turricula crumpii* Pilsbry; *Trophonopsis echinus* (Dall); *Japonacteon archibenthicola* Habe. Gravels from such depths are not covered by calcareous algae.

This archibenthic assemblage almost agrees with that found from similar depths near Omurodashi reported by Igarashi and Kurata (1956). As has been stated, the molluscan community on the islands near the banks under study is allied to those from neighboring banks; while, out of biological dredge samples from stations lower than that, at a depth of 470–480 m, near Hachijo Island, a different archibenthic molluscan assemblage is found ("Soyo" sta. B3, March

20, 1958, 33° 07.5' N, 140° 03.2' E, 480 m and do. Nov. 17, 1958, 33° 10.0' N, 140° 02.7' E, 470 m): *Fusinus?* sp.; *Trophonopsis echinus* (Dall); *Neptunea constricta* (Dall), var.; *Benthovoluta* sp.; *Conus* sp. nov. The bottom is found to be of volcanic gravel which is not coated by algal matter.

SUMMARY AND CONCLUSION

As the result of examination of biological dredge samples taken from submarine banks around the Izu Islands, it became clear that possible characteristic banks-associated molluscan assemblages are found in this area. Since they are closely associated with the bottom nature and the depth of the banks, the assemblages are composed mostly of the hard-bottom lower shelf fauna found on the southwestern Pacific coast of the Japanese main islands.

The present material was collected at random with various kinds of gear, so that a quantitative analysis of the fauna was not possible. However, constant occurrence and relative abundance of certain species were assumed as indicators of the fauna of the areas. The typical banks-associated molluscan assemblages from the Izu Islands area are possibly represented by such gastropods as *Perotrochus beyrichii*, *Galeoastrea guttata*, and *Tenagodus anguinus*, together with several pelecypods such as *Acar congenitum*, *Arca manila takii*, *Hawaiarca uwaensis*, *Samacar pacifica*, *Mimarcaria aizoi*, *Tucetona shinkurosensis*, *Chlamys vesiculosus*, *C. tissotii*, *C. lemniscata*, *C. mollita*, *Spondylus anacanthus*, *Plicatula muricata*, and *Lima fujitai*.

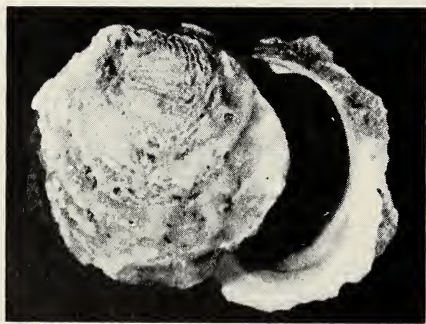


FIG. 17. *Chama argentata* Kuroda and Habe from insular shelf of Takeshima Is., 11.6 mm $\times$ 10.1 mm.



FIG. 18. *Spondylus anacanthus* (Mawe) from Uji Islet, 126 m, 40.2 mm $\times$ 37.5 mm.

The geographical difference of the assemblage within the area is not so obvious, but it is clear that the insular shelf fauna is substantially the same as that under discussion. It seems that the species found in the area are those distributed also in warmer districts. This impression may be corroborated by facts such as these:

- 1) Similar banks-associated assemblages are found in southern waters off Kyushu which are much more subtropic in average climate.
- 2) *Tucetona hanzawai* and *Samacar pacifica*, which are found from the Izu Islands area, were originally described by Nomura and Zimbo (1934) from the Ryukyu Limestone of Kikaijima (or Kikai-ga-shima), an island located far to the southwest of the Osumi Group. Concerning the fossil fauna found from this Ryukyu Limestone, Nomura and Zimbo cited Yabe and Hanzawa's opinion that the Ryukyu Limestone was deposited in waters warmer than are found there at the present time, and that fossils found there are very similar to the recent fauna found around the

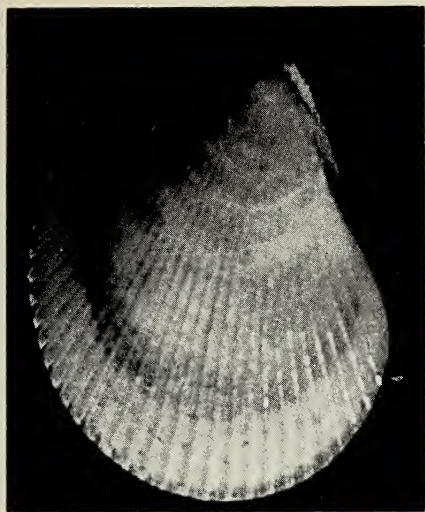


FIG. 19. *Lima fujitai* Oyama from Hyotanse, 118 m, 15.5 mm $\times$ 12.0 mm.

Ryukyu Archipelago, which is situated farther south than Kikaijima Island.

- 3) *Striarca fausta* is another example described from a fossil bed (at Moeshima in Kagoshima Bay, Kyushu) containing warmer water species.
- 4) Some elements of tropical origin are found in the banks fauna, e.g., *Chicoreus superbis*, which has been known from the

Bonin (or Ogasawara) Islands, and *Arca mauii takii*, which is presumably an endemic form of a Hawaiian species. These two species are found at Kurose, which is the most southern bank in the area.

An assumption that the molluscan assemblage of the Izu Banks is an isolated shelf fauna representing species derived from warmer water corresponds to that of Parker and Curray (1956: 2438) for the Gulf of Mexico. They concluded from their studies that the banks-associated molluscan assemblages in waters off Texas represented a population now isolated from the main centers of abundance ranging from southeast Florida to the West Indies and different from the surrounding level-bottom communities.

According to Teramachi (personal communication), there are some distributional gaps of upper-shelf mollusca even within the warm Kuroshio area, though they are far less conspicuous than those existing at about 36° N on the Pacific coast of Honshu. One such type of gap presumably is found around Ashizuri-Saki, for instance. The distributional difference of certain species of *Fusinus*, *Siphonalia*, *Ancilla*, and *Fulgoraria* off the east and west coast of the cape (about 34° 42' N, 133° E) may be found there. Regardless of this fact, the typical

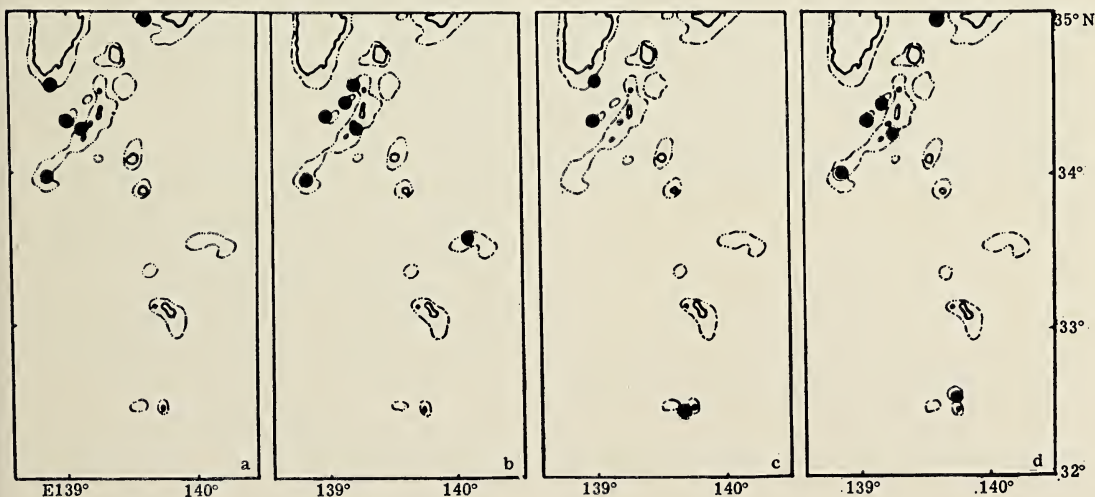


FIG. 20. Distribution of bank-associated mollusca. a, *Galeostraea guttata*; b, *Tuccetona shinkurosensis*; c, *Chama argenteata*; d, *Spondylus anacanthus*-*Lima fujitai*-*Plicatula muricata* (or any two of these).

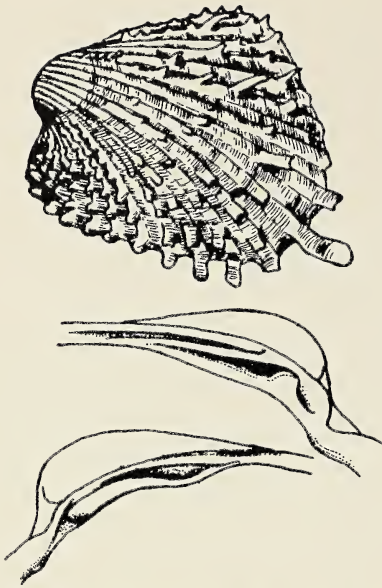


FIG. 21. *Glans kyushuensis*, sp. nov. (holotype), 16.0 mm $\times$ 13.0 mm $\times$ 5.5 mm.

banks-associated molluscan assemblages are found from the discontinuous biotopes, i.e., southwestern Kyushu (about $129^{\circ} 30' E$) and Izu Islands areas (about $140^{\circ} E$). Latitudinally, they are distributed from the southern tip of Izu Peninsula ($34^{\circ} 34' N$) southward to Torishima Island ($30^{\circ} 30' N$).

Above all, this study shows how marine mollusca on the same level under similar ocean climate are governed in their distribution by the substratum. Moreover, a particular molluscan assemblage (or simply a combination of the species) can serve to indicate the sedimentary characteristics of the banks in the Kuroshio area.

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APPENDIX

Glans kyushuensis Okutani, sp. nov. (Carditidae)

Shell equivalve, closed, stout, gibbous in

shape; quadrangular in outline; beak anteriorly oblique; surface rough, uniformly pink in color, sometimes with delicate wavy pattern of darker color on posterior region; radial ribs running from umbo to distal margin, 20 or 21 in number, as wide as shallow interspacial grooves, granulated on anteroventral ones, while sparsely spinose on rest; longest spinose scale as long as $\frac{1}{5}$ of shell length; escutcheon narrow; lunule deeply impressed, cordate in outline.

Interior smooth, with shallow radial grooves; ashy white with pinkish tint; on right valve, anterior cardinal teeth vestigial, while posterior ones elongated; on left valve, anterior cardinal teeth short, small but prominent, posterior ones elongated, plate-like in shape; ventral margin crenulated; mantle scar smooth.

LOCALITY: $35^{\circ} 50' N$, $130^{\circ} 28.5' E$, 210 m in depth, gravels and shell.

TYPES: Left odd valve: 16 mm long, 13 mm high, 5.5 mm thick (holotype). Left odd valve: 13 mm long, 11.5 mm high, 5 mm thick (paratype). Right odd valve: 18 mm long, 16 mm high, 7 mm thick (paratype).

REMARKS: This new species is closely allied to *G. hirasei* (Dall),² but the latter has more radial ribs which are closely scaly. This new species is distinguished from *G. millegranosa* (Nomura and Zimbo),³ which has a strongly inflated shell and granulated radial ribs.

DISTRIBUTION: The type locality and off Kii Peninsula (collected by Mr. Teramachi; conjoined valve measures $24 \times 20 \times 18$ mm).

² Dall, 1918: Proc. U. S. Nat. Mus. 54(2234): 234.

³ Nomura and Zimbo, 1934: Sci. Rept. Tohoku Imp. Univ., 2nd ser., 16(2): 154(45), pl. v(i), figs. 13a, b, 14a, b. Also Okutani, 1958: Venus 20: 220, tfs. 2, 3.

Notes on the Osteology and Systematic Position of *Hypoptychus dybowskii* Steindachner and Other Elongate Perciform Fishes¹

WILLIAM A. GOSLINE²

LONGER AGO that can gracefully be admitted, Dr. Paul Kähnsbauer of the Vienna Naturhistorische Museum was kind enough to send me a specimen of *Hypoptychus dybowskii* from Steindachner's (1880) original series taken off "Northern Japan." Steindachner placed this fish alongside the Ammodytidae, and there has been a division of opinion ever since as to whether it should be included in or excluded from that family (cf. Regan, 1913; Jordan, 1923; Duncker and Mohr, 1939; Berg, 1940). In order to investigate its relationships, the Vienna specimen has been stained and dissected, and its osteology compared with that of the ammodytids *Bleekeria gilli* (Fig. 1a) and *Ammodytes tobianus*. The specimen of *Bleekeria* is Hawaiian and was retrieved from tuna spewings. *Ammodytes* is represented by two series, sent to me from the U. S. National Museum and the Museum of Comparative Zoology through the courtesy of Dr. L. P. Schultz and Dr. G. W. Mead, respectively.

That *Hypoptychus* belongs to the superfamily Ammodytoidea seems certain. The relationships of the superfamily Ammodytoidea are more obscure. A second objective of the present investigation has been to look into this matter, and a preliminary discussion of certain of the problems involved here will serve as an introduction to the paper.

In a typical percoid fish, e.g., *Epinephelus*, there are 24 vertebrae, and the dorsal fin is composed of an anterior spinous portion and a posterior soft portion. In such a fish the majority of the basal supporting elements, i.e., pterygiophores, of the spinous dorsal have a one-to-one relationship with the vertebrae below them; the soft dorsal rays and their ptery-

giophores, in contrast, are more closely spaced so that there is more than one ray and pterygiophore to each vertebra. Time and again, however, the percoids and their derivatives have become elongate. This change in shape is frequently accompanied by a whole series of other alterations. Thus, the cranial crests become low or disappear, the number of vertebrae increases, the distinction between dorsal spines and rays becomes reduced, both types of dorsal (and anal) rays develop an approximately one-to-one relationship with the vertebrae, and the caudal fin becomes rounded and its principal rays reduced in number. All of these changes are to be found among the percoids, e.g., the Cepolidae, trachinoids, ammodytoids, blennioids, schindlerioids, and most gobioids.

Indeed, it seems that all of these modifications occur together in the majority of elongate percoid derivatives and that those forms, such as the ophidioids, where there is more than one dorsal and anal ray per vertebra are the exception rather than the rule. On the other hand, the author is aware of no prepercoid teleost with a one-to-one relationship between soft dorsal and anal rays and the vertebrae. If what has just been said is correct, it follows that any fish with such a relationship is a percoid derivative, but that the unit correspondence between soft rays and vertebrae is of little use in distinguishing the various lineages of percoid derivation.

Here, the schindlerioids and gobioids will be dismissed from further consideration, as each of these groups has peculiarities by which it may easily be defined. However, Hawaiian specimens of the trachinoids *Parapercis schauinslandi* (Parapercidae, Fig. 1c) and *Crystallodytes cookei* (Trichonotidae, Fig. 1b), and of the blennioid *Tripterygion atriceps* (Tripterygiidae, Fig. 1d) have been stained and dissected. These specimens will be used both for purposes of com-

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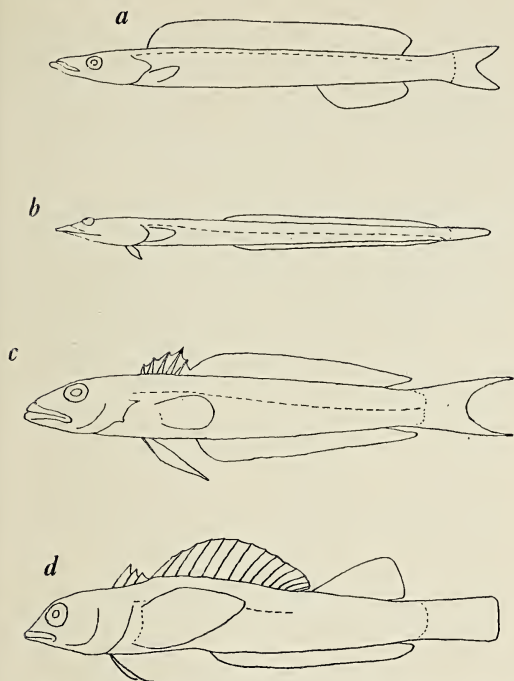


FIG. 1. Sketches of *a*, *Bleekeria gilli*, from Gosline and Brock, after Fowler, based on a specimen 3 inches in total length; *b*, *Crystallodytes cookei*, based on a specimen 2 inches long; *c*, *Parapercis schauinslandi*, from a 3-inch specimen; and *d*, *Tripterygion atriceps*, from a 1-inch fish.

parison with the three ammodytoids and in an attempt to obtain some understanding of the lineages to which each of them belongs.

With regard to these six fishes that have been investigated in some detail, it may be stated in advance that the author has not had any great success in discovering significant cranial differences between them. It is not so much that such differences do not exist, as that they appear to have rather slight systematic value. Though it may be that the author has simply overlooked significant differences, it would appear that the percoids and their immediate derivatives have a rather standardized skull pattern and that the major morphological differentiation of percoid groups has occurred in other features.

HEAD SKELETON

CIRCUMORBITAL BONES: In the typical percoid the circumorbital series is made up of the

lacrimal (preorbital) followed by about five separately movable, canal-bearing ossicles (cf, Katayama, 1959: figs. 2–5). Above the fifth, the infraorbital lateral line canal joins the supraorbital canal. Of the five ossicles the uppermost is particularly variable and is sometimes fused to and sometimes free from the sphenotic.

In *Parapercis* (Fig. 2*a*) the infraorbital canal is complete, passing through a lacrimal and six separate circumorbital bones. The uppermost of these is firmly attached to the cranium in *Parapercis*. Because six circumorbitals appeared to be a high number, the opposite side of the same specimen and of a larger specimen of *Parapercis schauinslandi* were checked; no variation was found. The circumorbital structures of *Tripterygion* differ from those of *Parapercis* in having three instead of six circumorbital bones and in the failure of the bone to close over the sensory canal externally. In *Crystallodytes* the circumorbital canal is still complete but there are only a lacrimal and two circumorbitals. The lacrimal and second circumorbital are large and laminar, but the anterior circumorbital is quite small.

In *Ammodytes* (Fig. 2*b*) there is a large lacrimal, followed immediately by a moderate-sized first infraorbital; then there is a broad gap followed by two small circumorbitals, the

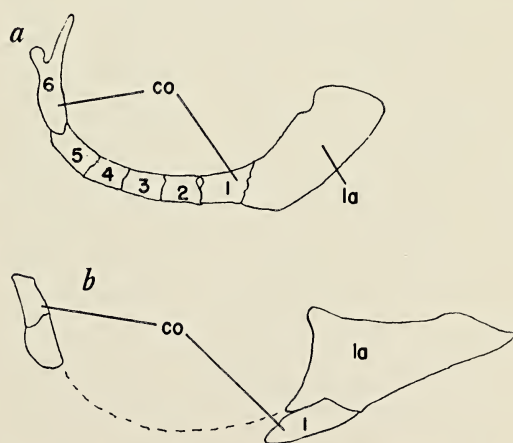


FIG. 2. Lacrimal and circumorbital bones of *a*, *Parapercis schauinslandi*, and *b*, *Ammodytes tobianus*. There are no circumorbital bones bordering the portion of the orbit indicated by the dashed line in *Ammodytes*. *co*, Circumorbital bones; and *la*, lacrimal.

upper of which articulates with the skull. In *Bleekeria* a similar break in the circumorbital ring occurs, but it is shorter than in *Ammodytes* and the posterior series seems to contain three or four small elements instead of two. *Hypoptychus* has the same two anterior elements followed by a broad gap; posteriorly, however, there is only a single ossicle, and it is fused to the sphenotic.

None of the six fishes have any subocular shelf from the circumorbitals.

JAWS: In sand-diving fishes like *Ammodytes* the mouth is usually not terminal; either it is withdrawn below an overhanging snout, as in *Crystallodytes*, or protected by a prognathous chin, as in *Ammodytes*. In *Ammodytes* the leading, lower jaw is firmly attached, but the upper has developed excessive powers of protrusion when the mouth is opened (van Dobben, 1935: 34-36). The great protrusibility of the upper jaw in *Ammodytes* is accompanied by a weakening of the bony elements, and it is probably in relation to this that *Ammodytes* and *Bleekeria* have edentulous premaxillaries. So far as jaw structure is concerned, *Hypoptychus* is intermediate between the normal percoid type and the specializations found in *Ammodytes* and *Bleekeria*.

The premaxillary of *Ammodytes* (Fig. 3a) consists of a long pedicel movably articulating at its base with the remaining portion of the premaxillary. The distal half of the maxillary tapers gradually to a point (Fig. 3a). The upper jaw of *Bleekeria* is essentially similar to that of *Ammodytes* except that a number of small ossicles are to be found in the ligamentous tissues connected with the jaw apparatus. Thus, there is an ossicle above the more lateral of the two pedicels of the premaxillary, another at the distal end of the premaxillary, and a whole series in the ligamentous tissue that runs between the upper and lower jaws.

The upper jaw of *Hypoptychus* (Fig. 3b) differs from those of *Bleekeria* and *Ammodytes* in the following features: the premaxillary bears a row of teeth (there are about 14 conical teeth in a single row on each side, not shown in Fig. 3b); the premaxillary is fused to its pedicel; and the tip of the maxillary is expanded distally.

A movable articulation between the pre-

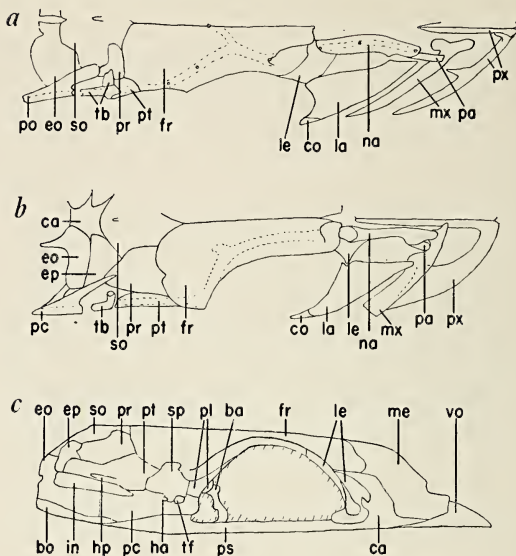


FIG. 3. Head skeletons of ammodytoids: superior views, with the premaxillary somewhat protruded, of a, *Ammodytes tobianus*, and b, *Hypoptychus dybowskii*; lateral view, c, of cranium of *Ammodytes tobianus*. ba, Basisphenoid; bo, basioccipital; ca, cartilage; co, circumorbital; eo, exoccipital; ep, epiotic; fr, frontal; ha, anterior hyomandibular socket; hp, posterior hyomandibular socket; in, intercalar; la, lacrimal; le, lateral ethmoid; me, mesethmoid; mx, maxillary; na, nasal; pa, palatine; pc, prootic; pl, pleurosphenoid; po, posttemporal; pr, parietal; ps, parasphenoid; pt, pterotic; px, premaxillary; so, supraoccipital; sp, sphenotic; tb, tabular; tf, trigemino-facial foramen; and vo, vomer. In the superior view of *Ammodytes*, a, the epiotic is covered by the posttemporal.

maxillary and its pedicel is also found in *Crystallodytes*, as well as in blennioids such as *Cirripectus* and *Istiblennius*. In *Parapercis* and *Tripterygion*, which have strong premaxillary teeth, the pedicel is stout and fused to the toothed portion.

GILL COVERS: In *Ammodytes* (Fig. 4b) and *Crystallodytes* (Fig. 4c) the subopercles are expanded, presumably to protect the throat region. Indeed, the lower border of the articular in *Crystallodytes* is greatly expanded below as well (Fig. 4c).

SUSPENSORIUM: The suspensorium of *Ammodytes* is specialized in a number of regards (Fig. 4b). Most notable among these is the elongated palatine strut. The whole length of this strut from its forward tip to its articulation with the quadrate is made up of the palatine

bone; the ectopterygoid is a minute triangular splint at the very base. In *Bleekeria* the structure of the suspensorium is essentially similar except that the ectopterygoid is somewhat larger so that the palatine does not meet the quadrate. The suspensorium of *Hypoptychus* (Fig. 4a) is a quite different structure. The palatine and ectopterygoid are about equal in size and are united to one another by a digitate suture. The metapterygoid is a small splint and the mesopterygoid appears to be absent.

Undoubtedly the greatest specialization in the suspensorium is that found in *Crystallo-*

dytes (Fig. 4c). Here the suspensorium is divided into two well-developed and strong portions with the ectopterygoid forming a long, delicate strut between them. In the anterior portion a large, firm mesopterygoid forms a shelf under a large part of the eyeball; it is firmly attached to the strong palatine anteriorly, but only by membrane to the ectopterygoid.

SKULL: In all of these fishes, there are no frontal-parietal crests, and the minute supra-occipital crest does not reach above the skull surface. *Tripterygion*, however, has a fringed, backwardly slanted crest running across the rear of the skull. This crest lies just behind the tabular ossicle on each side which bears the apparently incomplete supratemporal sensory canal commissure. (In the related *Entomacrodus* the supratemporal commissure is almost completely enclosed in the skull. Laterally, the commissure passes through a tabular ossicle that is fused to the cranium and thence medially through the rear of the parietals, leaving a large opening on the middorsal line.)

In *Parapercis* and *Tripterygion* the crania are somewhat more highly arched over the orbit than in the others. Probably in association with this, the wings of the parasphenoid extend farther up the sides of the postorbital bar than in the remaining four fishes. In all, however, the prootic extends over the top of the parasphenoid wings to the edge of the orbit. (In *Istiblennius*, related to *Tripterygion*, the parasphenoid wings meet the frontals in the usual blennioid fashion.)

In *Ammodytes* and *Bleekeria* the two exoccipital condyles lie adjacent to one another and form the upper portion of the facet for the articulation of the convex head of the first vertebra. In the other forms, including *Hypoptychus*, the exoccipital condyles lie at either side of the basioccipital articulation; the two exoccipital bones do not meet below the foramen magnum; and there is no rounded articular head on the first vertebra.

GILL ARCH SYSTEM: In *Ammodytes* the branchiostegal ray count is 8–7; in *Crystallodytes*, 7; in *Bleekeria*, 7; in *Parapercis* and *Tripterygion*, 6; and in *Hypoptychus*, 4–4.

In all the fishes under consideration the lower pharyngeals are separate. *Ammodytes* and

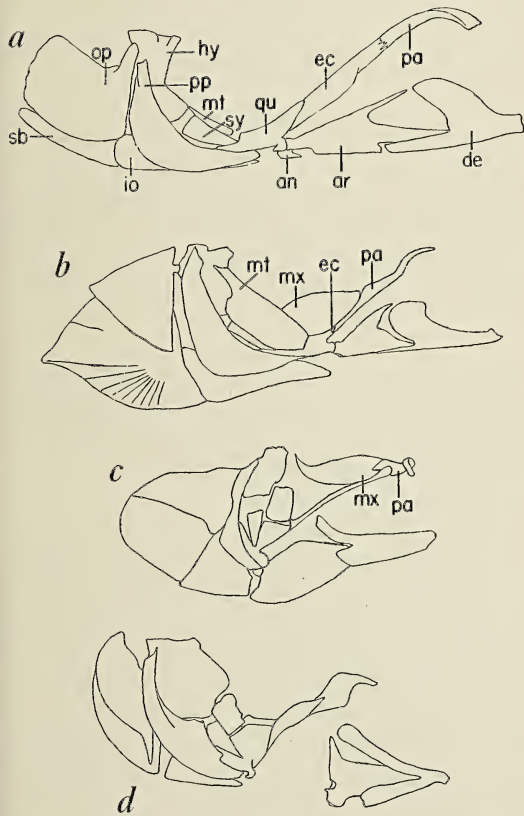


FIG. 4. Right gill covers, suspensoria, and lower jaws, external view, of a, *Hypoptychus dybowskii*; b, *Ammodytes tobianus*; c, *Crystallodytes cookei*; and d, *Tripterygion atriceps* (with the lower jaw dislocated). an, Angular; ar, articular; de, dentary; ec, ectopterygoid; hy, hyomandibular; io, interopercle; mt, metapterygoid; mx, mesopterygoid; op, opercle; pa, palatine; pp, preopercle; qu, quadrate; sb, subopercle; and sy, symplectic.

Bleekeria appear to be the only forms with 3 distinct upper pharyngeals on each side; *Hypoptychus* has separate upper pharyngeals on arches 2 and 3, but appears to have none on arch 4. *Parapercis* and *Crystallodytes* also have two pairs of upper pharyngeals, but the posterior pair seems to represent a combination of pharyngobranchials 3 and 4. *Tripterygion* appears to have only a single set of upper pharyngeals.

FINS, FIN SUPPORTS, AND AXIAL SKELETON

ANAL FIN: In the six fishes under consideration there is never more than a single unsegmented ray at the front of the anal fin, and even this is lacking in *Crystallodytes* and *Ammodytes*. All of the remaining anal rays are branched in *Parapercis*, some in *Hypoptychus*, only the last in *Tripterygion*, and none in *Crystallodytes*, *Bleekeria*, and *Ammodytes*.

Unlike the other three fishes, there is in the three ammodytoids a well-developed caudal peduncle behind the base of the last anal (and dorsal) ray; this is supported by about five vertebrae with bladelike neural and hemal arches.

DORSAL FIN: *Parapercis* and *Tripterygion* are the only fishes under consideration that have spinous dorsals. Furthermore, in these two the dorsal fins commence farther forward (over the 3rd vertebra in *Parapercis*, Fig. 5a, the rear of the skull in *Tripterygion*, Fig. 5b) than in the others (over the 5th vertebra in *Bleekeria*, and still farther back in the remaining forms). Structurally the spinous dorsal fin differs considerably in *Parapercis* and *Tripterygion*. In *Parapercis* it appears that the spinous dorsal has undergone some condensation, possibly as a result of forward movement of the soft dorsal, for the pterygiophores of the five spines interdigitate between neural arches 2 and 5 (Fig. 5a); one supraneural remains (rather than the three usually found in the lower percoids). In *Tripterygion* there are two spinous dorsals, the first of 3 spines and the second of 14; it appears very much as if the anterior 3 have appropriated the usual percoid supraneurals as their supporting bases. In the structure of the pterygiophores supporting the dorsal spines, *Parapercis* is considerably more generalized than *Tripterygion*.

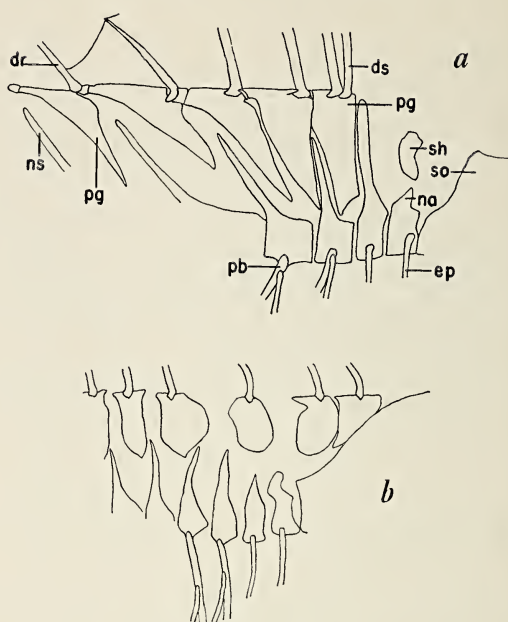
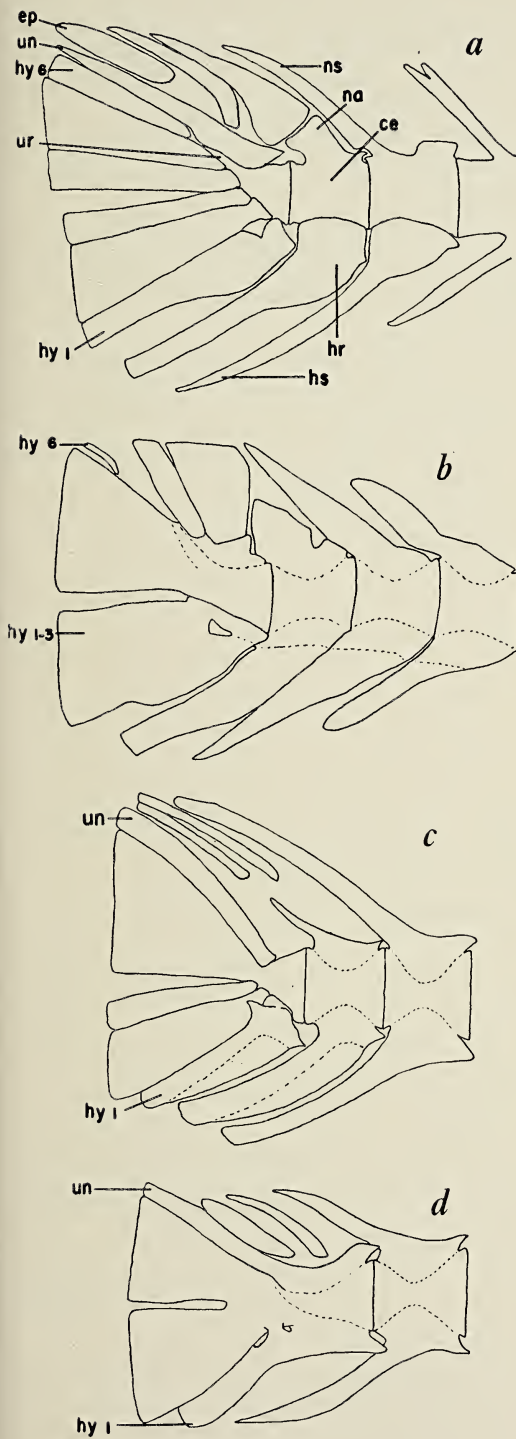


FIG. 5. Anterior vertebrae, ribs, dorsal rays and their supports in *a*, *Parapercis schauinslandi*, and *b*, *Tripterygion atriceps*. *dr*, Dorsal soft ray; *ds*, dorsal spine; *ep*, epipleural rib; *na*, neural arch; *ns*, neural spine; *pb*, pleural rib; *pg*, pterygiophore; *sh*, supraneural; *so*, supraoccipital.

In *Parapercis* the pterygiophores of the spines (except that of the first 2) retain their basic bisegmental structure (Fig. 5a); whereas in *Tripterygion* each pterygiophore is a fused monolithic unit (Fig. 5b).

In the soft dorsal, as in the anal, all the rays are branched in *Parapercis*, some in *Hypoptychus*, only the last in *Tripterygion*, and none in *Crystallodytes*, *Bleekeria*, and *Ammodytes*. In soft dorsal structure, there are again certain differences between *Parapercis* and *Tripterygion* on the one hand, and *Crystallodytes* and the ammodytoids on the other. In the first place, *Parapercis* and *Tripterygion* have the last dorsal (and anal) ray cleft to the base; *Crystallodytes* and the ammodytoids do not. Second, the pterygiophore of each soft dorsal ray in *Parapercis* and *Tripterygion* interdigitates deeply between a pair of neural spines (Fig. 5a), and there is an exact correspondence between vertebrae and soft dorsal rays. In *Crystallodytes* and the ammodytoids the pterygiophores of the soft dorsal (and anal) rays are short, weak structures



that interdigitate little if at all between the tips of the neural spines, and there is a rough but inexact correspondence between soft dorsal (and anal) rays and vertebrae.

CAUDAL FIN: The tails of the ammodytoids are somewhat forked, those of the other fishes under investigation more or less rounded. In all, there is a reduction in the caudal ray number from the typical percoid count of 17 principal rays, 15 branched. In *Parapercis* there are 15 branched rays, but no outer principal unbranched rays. In *Ammodytes* and *Bleekeria*, there are 15 principal rays, 13 branched. In *Hypoptychus*, there are 13 principal rays; apparently 11 of these were branched, but since the fin rays of the available specimen are broken the branched ray count cannot be definitely established (the same is true of the dorsal, anal, and pectoral fins). *Tripterygion* and *Crystallodytes* have 10 principal rays, 8 branched.

With regard to the caudal skeleton, *Parapercis* (Fig. 6a) is quite typically percoid (Gosline, 1961). There are six separate hypurals, one uroneural, and three epurals; none of these elements are fused to the urostyle. In the caudal skeleton of the other five fishes, considerably more fusion and/or reduction has occurred. Hypurals 4 and 5 are always fused with the urostyle, and, in *Crystallodytes* (Gosline, 1955: fig. 7d) and *Hypoptychus* (Fig. 6d), two or three of the lower hypurals as well. (Fig. 6d must be viewed with some reservation, as the specimen from which it was drawn may have been aberrant in having the last two vertebrae fused.) There are two epurals in *Tripterygion* (Fig. 6b) and the three ammodytoids, and only one in *Crystallodytes*.

PECTORAL FIN: The total number of pectoral rays in the fishes investigated is 15 in *Tripterygion* and *Parapercis*, 13 in *Ammodytes* and *Bleekeria*, 12 in *Crystallodytes*, and 9 in *Hypoptychus*. Of these, all are segmented in *Tripterygion* and the ammodytoids; however, there is a small, unsegmented, splintlike upper-

FIG. 6. Caudal skeletons of a, *Parapercis schauinslandi*; b, *Tripterygion atriceps*; c, *Bleekeria gilli*; and d, *Hypoptychus dybowskii*. ce, Centrum; ep, epural; hr, hemal arch; hs, hemal spine; hy, hypural; na, neural arch; ns, neural spine; un, uroneural; and ur, urostyle.

most ray in *Parapercis* and *Crystallodytes*. Judging from the material available, it appears that the uppermost pectoral ray is homologous whether splintlike or segmented, for it has the same very peculiar basal structure. Like other soft rays it consists of two halves. However, in the uppermost pectoral ray the two halves are usually not mirror images of one another. Rather, the scapula articulates with a facet that lies entirely on the inner "half" of the ray (except, among the fishes investigated, in *Hypoptychus* and *Tripterygion*). An inquiry into this peculiarity has shown that the scopeliform genus *Synodus* has a small bony nodule that lies between two equal halves, but is attached to the inner. As Starks (1930: 238) noted,

this nodule probably represents a modified actinost, which in many higher teleosts became incorporated into the inner, articular "half" of the uppermost pectoral ray (Fig. 7b, d).

The pectoral girdles of *Tripterygion* and of the ammodytoids are shown in Fig. 7. Those of the ammodytoids are peculiar in having the supracleithra and cleithra more or less vertically aligned.

There are two postcleithra in *Parapercis*, *Tripterygion*, *Ammodytes*, and *Bleekeria*, and apparently not any in *Crystallodytes* and *Hypoptychus*.

PELVIC FIN: Pelvic fins are lacking in the three ammodytoids studied here. However, two splintlike pelvic girdle elements are to be found in *Bleekeria* (Fig. 7b), and a small pelvic fin of a spine and three rays, located somewhat ahead of the pelvic bases, occurs in the related ammodytid genus *Embolichthys* (Jordan, 1902). The three other fishes studied here also have the pelvics originating ahead of the pectoral bases. *Parapercis* has a pelvic spine and five branched rays, the fourth considerably the longest. *Crystallodytes* has a short pelvic consisting of a spine and five unbranched but segmented rays. In *Tripterygion* there are two well-developed unbranched, but segmented, rays; there is no spine. In all three fishes the pelvic girdle articulates anteriorly with the cleithra. In *Crystallodytes* (Fig. 8d), the two halves of the pelvic girdle are rather widely separated anteriorly; in *Parapercis* (Fig. 8b) they are united for nearly their entire length; in *Tripterygion* (Fig. 8c) the two halves are not only united, but anteriorly they seem to have completely fused. Furthermore, *Tripterygion* has the pelvic girdle firmly wedged between the cleithra.

VETEBRAL COLUMN AND RIBS: *Parapercis* has 30 (10 + 20) vertebrae (including the urostyle); *Tripterygion*, 34 (10 + 24); *Crystallodytes*, 55 (29 + 26); *Ammodytes lanceolatus*, according to Regan (1913: 137), 69 (40 + 29); *Bleekeria gilli*, according to Duncker and Mohr (1939: 13), 57 (32 + 25); and *Hypoptychus*, 55 (31 + 24).

In *Parapercis*, *Tripterygion*, *Ammodytes*, and *Bleekeria* there are two sets of ribs. The lower, or pleural, ribs start from the 3rd vertebra; the upper, or epipleural, ribs start from the 1st,

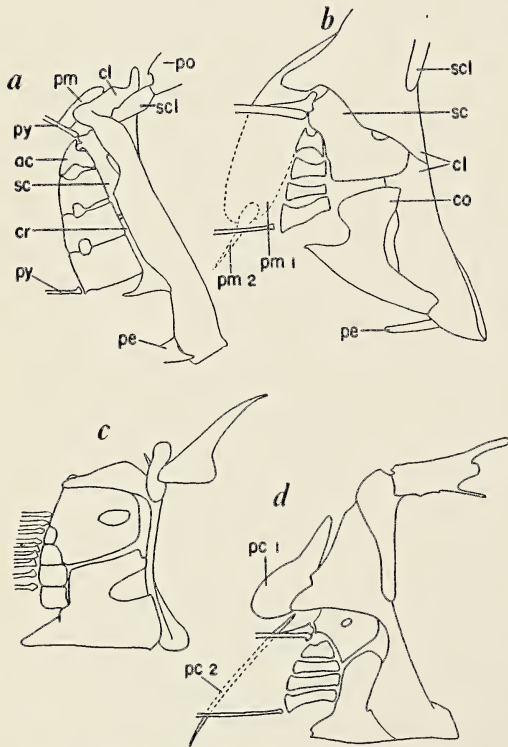
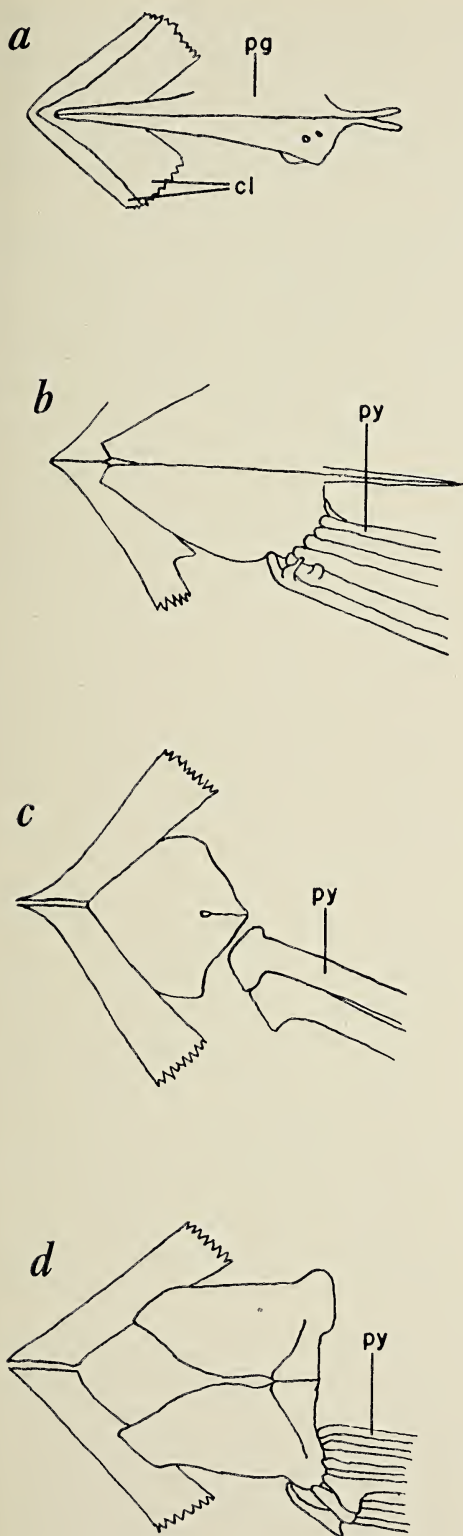


FIG. 7. Right pectoral girdles, external view, of a, *Tripterygion atriceps*; b, *Bleekeria gilli*; c, *Hypoptychus dybowskii*; and d, *Ammodytes tobianus*. Only the uppermost and lowermost pectoral rays are shown in a, b and d; the top of the pectoral girdle is not drawn in b; and the lower postcleithrum is not indicated in a. ac, Actinost; cl, cleithrum; co, coracoid; pc, postcleithrum; pe, pelvic girdle; pm, postcleithrum; py, pectoral ray; sc, scapula; and scl, supracleithrum.



articulating with the upper surface of the pleural ribs from the 3rd vertebra on (Fig. 4a, b). In *Crystallodytes* there is only one set of ribs which starts with the 1st vertebra; this set would appear to represent the epipleurals. In *Hypoptychus*, there is also only one series of ribs, but it starts from the 3rd vertebra and would appear to represent the pleural series.

DISCUSSION

On the basis of osteological characters, *Parapercis*, *Crystallodytes*, *Tripterygion*, and the three ammodytoids could be grouped in a number of ways. One such system would separate the more elongate forms, i.e., *Crystallodytes* and the ammodytoids, from the shorter, stockier *Parapercis* and *Tripterygion*. Such a division could be expressed osteologically as follows.

Parapercis and *Tripterygion*. Premaxillary pedicels stout, firmly fused to the toothed portions. Wings of the parasphenoid expanded, forming the lower portion of the postorbital bar. The abdominal portion of the vertebral column shorter than the caudal portion, consisting of 10 vertebrae. Dorsal with an anterior spinous portion which commences over or ahead of the 3rd vertebra. Last dorsal and anal rays cleft to their bases. Pterygiophores of the dorsal and anal rays deeply interdigitating between successive neural and hemal spines, respectively.

Crystallodytes and the ammodytoids. Premaxillary pedicels long and/or movably articulated with their lateral portions. Wings of the parasphenoid little developed, not extending up as a portion of the postorbital bar (Fig. 3c). The abdominal portion of the vertebral column longer than the caudal portion, of more than 10 vertebrae. No spinous dorsal, the soft dorsal commencing over or behind the 5th vertebra. Last dorsal and anal rays undivided. Pterygiophores of the dorsal and anal rays interdigitating little or not at all between the neural and hemal spines, respectively.

To group the fishes under consideration in

FIG. 8. Pelvic girdles, from above, of a, *Caranx ignobilis*; b, *Parapercis schauinslandi*; c, *Tripterygion atriceps*; and d, *Crystallodytes cookei*. The pelvic rays are not indicated in a. cl, Cleithrum; pg, pelvic girdle; and py, pelvic ray.

the above fashion is to separate those nearer the generalized percoid type from those that are more specialized. Such a division may merely represent levels of structural organization rather than relationships.

Parapercis is much the least differentiated from the typical percoids of any of the six fishes dealt with in this paper. All of the remaining five fishes (*Tripterygion*, *Crystallodytes*, *Ammodytes*, *Bleekeria*, and *Hypoptychus*) have in common the following specializations over and beyond those found in *Parapercis*: circumorbital series of bones incomplete or complete and consisting of a lacrimal and only 2 or 3 circumorbitals; no pungent dorsal spines; caudal with 13 or fewer principal rays; urostyle fused to the upper hypurals; pelvics reduced (i.e., without branched rays) or absent.

Most of the minor specializations that *Parapercis* does exhibit seem to be associated with fin structure. Thus the pelvics are advanced in position and have the inner (actually the 4th) soft rays the longest, but there appears to be no great specialization of the pelvic girdle (Fig. 8*b*). The caudal fin lacks the usual principal unbranched rays, though the caudal skeleton is typically percoid (Fig. 6*a*). The spinous portions of the dorsal and anal have been reduced. In the anal there is a single small unsegmented splint at the front of the fin. The spinous dorsal seems to have been pushed forward and concentrated as well as reduced in size, for there is only one supraneural and the pterygiophores for all five spines extend between neural arches 2 and 5. The soft dorsal and anal retain a typical percoid condition. However, their pterygiophores interdigitate deeply between successive neural and hemal spines and bear a one-to-one relationship with the vertebrae. Now in typical percoid families, though not apparently in the Cepolidae, the soft dorsal and anal rays usually do not interdigitate deeply between the neural and hemal spines, and there are usually about two pterygiophores per vertebra. This is true of even fairly elongate forms like the goatfish, *Mulloidichthys samoensis*. To change this arrangement to a one-to-one relationship between pterygiophores and vertebrae requires either an increase in the spacing between soft dorsal and anal rays, or an increase in the number of verte-

brae, or both. The cigar-shaped labrid *Cheilodactylus inermis* seems to be an instance where a one-to-one ratio has been brought about by increased spacing between rays, for this fish retains 24 vertebrae. In most elongate fishes, however, an increase in vertebrae has also taken place.

On the basis of *Parapercis* alone it is impossible to evaluate Regan's (1913) percoid "Division Trachiniformes" (equals superfamily Trachinoidea). Suffice it here to remark that there does appear to be a somewhat extensive group of usually rather deep-water bottom fishes having essentially the fin characters described above for *Parapercis*. Whether these fishes are really related is impossible to say at this point. The relationship of *Crystallodytes* to this group is also doubtful. Certainly *Crystallodytes* represents a much higher degree of differentiation from the typical percoids than *Parapercis*. (For certain characteristics of *Crystallodytes*, see below.) Some knowledge of less specialized (or at least of other) forms of the *Crystallodytes* lineage should provide far better indications of its relationships than are available from a study of this form alone. (Throughout this paper, *Crystallodytes* has been considered a trichonotid, but that this is a correct family allocation is dubious, cf. Schultz, 1960: 273.)

Tripterygion is generally agreed to be a member of the perciform suborder Blennioidei. However, this suborder, since it was defined and later restricted by Regan (1912, 1929), has undergone considerable disintegration and rearrangement (Starks, 1923; Smith, 1952; Hubbs, 1952; Gosline, 1955; and Makushok, 1958). Even after certain nonblennioid groups have been removed, Hubbs and Makushok feel that most or all of the remaining families may be divided into a northern (cold water) group and a southern (warm water) group which may have had independent origins among the percoid families.

Tripterygion is, in many respects, one of the more generalized, i.e., percoid, members of the whole warmwater group. This group differs radically from the remaining fishes under consideration here in its mode of life. The southern blennies characteristically use their thickened pelvic rays to prop the anterior end of the body

away from the hard substratum on which they feed. The more elongate forms at least characteristically rest with the tail bent, and, when disturbed, retreat into holes in the rock and coral by means of sinuous movements of the body. A number of the characteristic external features of the southern blennies are probably associated with this mode of life. For example, the pelvic rays though reduced in number are stout, and are attached to a short pelvic girdle that is firmly wedged between the wings of the cleithra. The dorsal fin extends far forward, in the extreme case of *Xiphasia* to above the eye. There is often a pair of tentacles or a transverse fringe of them, e.g., *Cirripectes*, on the nape; in *Tripterygion* there is a low transverse fringe across the nape in exactly the same position as in *Cirripectes*, but it is made up of bony flaps extending upward from the skull.

A few other characters of *Tripterygion atriceps* may be mentioned because of their bearing on blennioid classification. The lateral line canal of the lacrimal and three circumorbitals is not covered by bone externally (Hubbs, 1952: 48, 50). A basisphenoid is present (Makushok, 1958: 58). The lowermost actinost in the pectoral girdle is not greatly longer than deep (Makushok, 1958: 58; compare Fig. 7a of the present paper with Makushok's fig. 25). Finally, in the caudal skeleton of *Tripterygion* (Fig. 6b) the three lower hypurals have fused to one another. Hypurals 4 and 5 (above the axis) have also fused to one another and to the urostyle and uroneurals. Hypural 6 is a small separate ossicle (the "minimum hypural" of Makushok, 1958), and there are two broad epurals. In the northern blennies, by contrast, the upper or epaxial hypurals are usually, though not always, separate from the urostyle (Makushok, 1958: 38, and fig. 22). Also, the northern blennioids usually have three epurals, rather than the two of *Tripterygion*. (In 1955: fig. 7f, I provided a sketch of the caudal skeleton of *Istiblennius gibbifrons*. I have not been able to relocate the specimen from which the drawing was made, but judging from specimens of *Entomacrodus marmoratus* and *Istiblennius zebra*, which have caudal skeletons very like that of *Tripterygion*, the figure is incorrect in showing a fusion of the lower hypurals and the

epurals with the rest of the urostyle vertebra.)

The investigation of *Tripterygion* reported on here would support, in its small way, Hubbs' (1952) and Makushok's (1958) thesis that the "northern" and the "southern" blennies are diphyletic. But whether they are diphyletic in the sense that the two groups have wholly different origins or in the sense that they have diverged in two different directions from the same or from two closely related stocks would seem to remain an open question. That *Tripterygion* has little relationship to the congrogadids (cf, Smith, 1952) also seems clear.

Among the more elongate fishes investigated, i.e., *Crystallodytes* and the ammodytoids, *Crystallodytes* and *Ammodytes* at least are sand divers. The pointed heads, long bodies, low vertical fins, small or absent pelvics, modified scales, and peculiarities of the lateral line of the body are probably associated with this mode of life. The habits of the other two ammodytoids, *Bleekeria* and *Hypoptychus*, are unknown.

That there is any phylogenetic relationship between *Crystallodytes* and the ammodytoids seems extremely doubtful. *Crystallodytes* differs immediately from the ammodytoids in the following characters. The lower jaw is included and the upper appears to be nonprotrusile. The circumorbital series of bones is complete. The cleithra are very oblique with the lower ends far forward of the upper. The dorsal and anal extend far back, and there is no well-demarcated caudal peduncle. Both the principal and procurrent fin rays are reduced in number. The lateral line runs low on the body posteriorly, just above the anal base. Finally there is a series of specializations related to the eye and suspensorium of *Crystallodytes*. In the first place, the eye itself is very characteristic, for *Crystallodytes* is a pop-eyed fish (Fig. 1b) with the small pupil protruding notably beyond the rest of the eyeball. This eyeball is supported below by a large and firm subocular shelf composed of the greatly expanded mesopterygoid. This bone, together with the palatine, forms a nearly separate portion of the suspensorium only weakly attached to the rest of this structure by the long, weak ectopterygoid (Fig. 4c). Neither the suspensorium nor the peculiar eyeball shows any relationship whatever to those structures in

Parapercis, which is typically percoid in these respects. Nor does *Crystallodytes* show any relationship to any of the other fishes investigated in these structures. Indeed, the only fishes that would seem to have a suspensorium anything like that of *Crystallodytes* are the congrogadids (cf, Regan, 1912: fig. 2b, and Smith, 1952: pl. 6B).

The three ammodytoid fishes may be defined as follows: elongate fishes with premaxillaries highly protrusile. Circumorbital bones incomplete, the lacrimal and first circumorbital separated from the rest of the series. Fins without spines or unsegmented rays except for the procurrent rays of the caudal (pelvic rays of *Embolichthys*?). Caudal forked or emarginate, preceded by a well-marked caudal peduncle which is supported by five or more vertebrae with bladelike neural and hemal spines. Pelvics absent (of a spine and three rays in *Embolichthys*, Jordan, 1902). Vertebrae 55 to 69, the abdominal vertebrae more numerous than the caudal, in approximately a one-to-one relationship with the dorsal and anal rays above and below them. Cleithra and supracleithra almost vertically aligned.

The analysis of *Hypoptychus* indicates that it is widely separated from *Ammodytes* and *Bleekeria*. Though the three genera hold a number of features in common it would seem that *Hypoptychus* has evolved in quite a different direction from the other two. Thus, while *Hypoptychus* remains more percoid in jaw structure and skull-vertebral column articulation, it has become more specialized (degenerate?) in almost every other feature: the bones are thin; the branchiostegal rays and fin rays are reduced in number; the scales have been completely lost; etc. *Hypoptychus* well warrants the separate family Hypoptychidae apparently first assigned to it by Jordan (1923: 230).

The families Hypoptychidae and Ammodytidae may be contrasted as follows.

Hypoptychidae. Scales entirely lacking. Jaws subequal, the premaxillary with teeth and with its long pedicel firmly attached. Branchiostegal rays 4. Articular facets of the exoccipitals widely separate. Dorsal and anal fins equal in length, of about 20 rays. Caudal with 13 principal rays; pectorals with 9.

Ammodytidae. At least some scales present. Lower jaw protruding, sharptipped. Premaxillary without teeth and with its pedicel movably attached to its lateral portion. Branchiostegal rays 7 or 8. Articular facets of exoccipitals contiguous. Dorsal extending far forward of the anal. Caudal with 15 principal rays; pectorals with 13.

The problem of ammodytoid origin remains obscure. The majority of features point to a percoid origin of some sort, but none of the percoid families known to the author would seem to provide a suitable ancestor.

The ammodytoids in turn would appear to have led to nothing with the exception of one highly speculative possibility. If the terminal vertebra of *Hypoptychus* is not merely the result of fusion in an aberrant specimen, then a progressive evolution along many of the lines already apparent in that fish might end in a neotenic form very like *Schindleria* (cf, Gosline, 1959).

Whatever the ancestors and derivatives of the ammodytoids may be, they remain, so far as known, sufficiently isolated and characterized to warrant fully the superfamily status among the Percoidei that has generally (cf, Regan, 1913) been assigned to them.

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Observations and Experiments on the Food Habits of California Sea Hares of the Genus *Aplysia*

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IN A PREVIOUS PAPER the senior author (Winkler, 1959a) presented the results of fecal pellet analyses to determine the influence of diet on the color of *Aplysia californica* Cooper. Only the dominant plants were mentioned in connection with that immediate problem. The present paper contains more detailed information from that study and from subsequent observations and reviews of references to *Aplysia* food plants.

The food of *A. californica* has received only limited consideration in connection with other studies. This is also true, however, of *Aplysia* species in general. Even in the large monograph of Mazzarelli (1893) the only indication of the nature of the food is in a discussion of the method of feeding, where we find the phrase "... algae (ordinarily *Ulva lactuca*) which serves as nutriment." In the extensive study of European *Aplysia punctata* by Eales (1921), about half a page is concerned with food. She notes an apparent change in food habits with age. The young, she says, live on red seaweed like *Delesseria* [probably *D. sanguinea*] and then slowly migrate through the *Laminaria* zone, where they feed on *Laminaria*, into shallow water, where the fully grown adults live on *Fucus* and *Ulva*. However, since she also states that they are found in the greatest numbers in the *Zostera* beds, it may be that like *Aplysia californica* they also feed on *Zostera*.

As to the feeding habits of *A. californica*, MacGinitie (1935) stated that the animal eats *Zostera* in Elkhorn Slough. In a later work (MacGinitie, 1949) he stated that they eat "seaweeds." Winkler (1959a) referred to three red

seaweeds used as food by *Aplysia californica* and to their effect on the color pattern. Another paper (Winkler, 1959b) mentions the effect of diet, both qualitatively and quantitatively, on the purple secretion. Winkler (1961) mentions diet in connection with two special habitats which are reported here in more detail. Marcus (1961) stated that *A. californica* eats seaweeds, "especially *Zostera* and *Codium*."

MATERIALS AND METHODS

Young specimens of *Aplysia californica* 4-5 inches long were captured on the central shore area of Lunada Bay, Palos Verdes, California, and each was placed in an individual pint fruit jar until fecal pellets were passed. The pellets were then removed to small screw-capped vials and the animal was released at sufficient distance to preclude resampling. Twenty-five specimens from this area were sampled in this manner. Pellets were also collected from larger specimens wandering in the deeper waters of the bay and from 1 mile north of the north side of Palos Verdes Point. The pellets were kept under refrigeration until examined and identified by the junior author. Since the efficiency of sea hare digestion appears to be in indirect proportion to the rate and quantity of food ingestion, identification of the algae offered no great problem since these sea hares were well fed.

Observations on specimens taken from Doheny Beach, California, and from a small lagoon at Lunada Bay, possessing a different flora than the former, are also reported. The food plants determined from crop contents were made during other studies involving the sacrifice of the animals.

RESULTS

Results from 25 young specimens taken from Lunada Bay in 1955 are presented in Table 1. In this area the following seaweeds were noted

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TABLE 1

DIET OF YOUNG *Aplysia californica* AT LUNADA BAY

KINDS OF PLANTS*	NO. SPECIMENS IN WHICH FOUND	NO. SPECIMENS IN WHICH DOMINANT
<i>Acrosorium uncinatum</i>	1	1
<i>Centroceras clavulatum</i>	8	4
<i>Ceramium eatonianum</i>	21	14
<i>Corallina vancouveriensis</i>	12	1
<i>Gelidium coulteri</i>	11	2
<i>G. crinale</i> (?)	7	1
<i>Gelidium</i> sp.	1	0
<i>Gigartina canaliculata</i>	14	7
<i>Hypnea valentiae</i>	4	2
<i>Lophosiphonia</i> sp.	1	0
<i>Phyllospadix</i> sp.	6	0
<i>Plocamium pacificum</i>	12	2
<i>Pterocladia</i> sp.	4	0
<i>Pterosiphonia</i> sp.	2	0
<i>Spermothamnion snyderae</i>	1	0
<i>Sphaelaria</i> sp.	2	0
<i>Ulva</i> sp.	2	0

* Although marked differences in the relative abundances of the various algae in the habitat would seem to negate the validity of this table in indicating selectivity of food by the sea hares, there is some interesting supporting evidence. Although *Gigartina canaliculata* was the dominant intertidal rock-cover alga throughout the area, and was eaten, it appeared far less dominant in the pellets than the small, relatively inconspicuous epiphytic alga *Ceramium*. Similarly, although *Ulva* and *Plocamium* were so sparse in the areas as generally to go unnoticed, these, especially the latter, appeared in the pellets.

to be common, though never found in the fecal pellets: *Laurencia splendens*, *Chondria californica*, *Gigartina leptorhynchus*, *Prionitis lanceolata*, *Laurencia subopposita*, *Cystoseira osmundacea*, *Gymnogongrus leptophyllus*, *Bossea orbigniana*, *Herposiphonia* sp., *Rhodymenia* sp., and *Colpomenia sinuosa*.

All specimens taken from deeper water in Lunada Bay and off Palos Verdes Point were similar in the algal content of their pellets. In every case the dominant plant was *Plocamium pacificum*, but with some admixture. These admixtures included *Phyllospadix* sp., *Lophosiphonia* sp., *Gelidium* (several species), and *Ceramium eatonianum*.

In May 1961 the larger red-striped *A. californica* from Lunada Bay were found feeding exclusively on the red alga *Laurencia pacifica*, which turned their blood and digestive glands a deep red.

Observations of the crop contents of several hundred *Aplysia* specimens were made during the course of work in 1959 at the Lunada Bay lagoon. Occasional spot checks were made in which the contents were determined as to species, but no single alga was recognized as dominant. The samples contained: *Chondria californica*, *Lithothrix aspergillum*, *Ceramium eatonianum*, *Centroceras clavulatum*, *Plocamium pacificum*, *Corallina gracillus*, and *Ectocarpus* sp., intermixed with fragments of coralline algae. The flora of this small lagoon contained more coralline algae and much less *Gigartina canaliculata* than the afore-mentioned 1955 collection site located ¼ mile to the south on Lunada Bay.

The collecting area at Doheny Beach was located at the extreme north end of the state park, where a small lagoon of uniformly shallow water is protected on the north by a stratified rocky peninsula submerged at higher tides, and on the south by a wave-formed reef of small boulders and gravel. The flora was comparatively limited, consisting predominately of various jointed coralline algae with intertwined *Hypnea valentiae*. Algal growth improved as one moved to the seaweed area of the lagoon. In this habitat 86 specimens were collected, but because of apparently grossly similar crop contents only 8 specimens were analyzed for presentation in Table 2. Collection dates were March 24, 1959, for numbers D-02 to D-08, and April 29, 1959, for the remainder. It will be noted that the latter collection shows a greater specialization of diet than the former and may reflect the concentration of sea hares farther out in the lagoon than at the former collection date. It may, on the other hand, suggest that the sea hare tends to become more selective in its food as it becomes older. This has generally been noted from other areas.

The algal contents of crops of *Aplysia vaccaria* have also been examined. Animals collected in their usual haunts in the *Egredia* beds have contained only large amounts of *Egredia* in their crops. On the other hand, when the animals are inshore in breeding aggregations the crops are usually empty or contain sand or other material of little significance. On one occasion only, several such animals were found

to have ingested a quantity of *Pelvetia fastigata*, a food plant that was consistently refused by aquarium-confined specimens (Winkler, 1955). The diet of the young of this species has not been determined.

DISCUSSION AND CONCLUSIONS

In northern California *Aplysia californica* is known principally from protected bays and estuaries such as Elkhorn Slough, Bodega Bay, and Tomales Bay. In these areas, beds of *Ulva* and *Enteromorpha* often occur abundantly, and J. J. Gonor has reported to us in a personal communication that *A. californica* lives in these beds and apparently uses both plants for food. Marcus (1961), reporting upon specimens from Bodega Bay and Tomales Bay, indicated that *A. californica* feeds on sea plants, especially *Zostera* and *Codium*. MacGinitie (1935) stated that sea hares in Elkhorn Slough fed on *Zostera*, but in subsequent personal correspondence has indicated that they also fed on *Enteromorpha*, which is sometimes the most prevalent plant in the slough. However, he also observed that at certain seasons the alga was absent from the area while *Zostera* remained. He concluded, then, that *Zostera* was their principal staple food.

In southern California the eel grass, *Zostera*, does not occur intertidally on the open coast and is uncommon in bays, and although the

similar surf grass, *Phyllospadix*, grows in profusion at low water levels it is rarely ingested by sea hares. Likewise, neither *Ulva* nor *Enteromorpha* is abundant in open coast habitats of southern California, and, although captive sea hares showed preference to *Ulva* or *Enteromorpha* over any other food offered them in the laboratory, in nature they resort to feeding on red algae, which are almost their exclusive food.

Young southern California sea hares seem to eat a wide variety of seaweeds depending upon the flora in their immediate surroundings, although some species are apparently habitually refused. As they grow older and wander farther they seem to become more selective in their food habits and develop a behavior pattern that is difficult to break under changed feeding conditions in the laboratory.

It has been generally observed that *Aplysia californica* in northern California is of larger average size than in southern California, and the senior author considers that this larger size, as well as the difference in color (Winkler 1959a), results from dietary differences. Experimental evidence for the variation in size similar to that for color variation is needed to confirm the homogeneity of the two forms. Two distinctive dietary factors offer themselves for study: (1) the comparative nutritive value of a high *Ulva-Enteromorpha* component in the diet during spring and summer; (2) the effect of almost exclusive feeding on the marine grass,

TABLE 2
PRESENCE AND RELATIVE ABUNDANCE OF SEVERAL ALGAE IN CROPS
OF *Aplysia californica* FROM DOHENY BEACH, CALIFORNIA

COLLECTION NO.	<i>Hypnea valentiae</i>	<i>Jania tenella</i>	<i>Corallina gracilis</i>	<i>Corallina pinnatifolia</i>	<i>Corallina vancouveriensis</i>	<i>Sphacelaria</i> sp.	<i>Laurencia</i> sp.	<i>Litothrix aspergillum</i>
D-02	××××	×						
D-04	××		××					
D-06	×	×××						
D-08	×	×	×	×		×	×	×
D-20	××××							
D-21	××××							
D-27	××××							
D-28	×××				×			

Zostera marina, during winter. Further studies are also needed on the diet of adult *Aplysia californica* which, according to Limbaugh (personal communication) are most numerous at depths of 30–40 ft and have been observed as deep as 100 ft, depending upon concentrations of plants. He mentions them eating the "thinner red and green seaweeds."

From evidence now available it would appear that *Aplysia californica* and *A. vaccaria* are not competitive for food, and that the former uses red and green algae as well as marine phanerogams for food, while the diet of the latter is essentially restricted to the brown alga *Egregia*, at least in the tidal zone. The nutritive value of *Egregia* seems to favor growth to large size, for Limbaugh has reported observations of specimens of *A. vaccaria* in the subtidal zone measuring up to 30 inches and an estimated 35 lb, making them the giants of the gastropoda.

SUMMARY

Young *Aplysia californica* on the open coast of southern California subsist on a diet mainly of fleshy red algae but show a preference for *Ulva* or *Enteromorpha* under artificial feeding. In the northern end of its range, where it appears to become largely estuarine in habitat, all reports indicate that it feeds almost exclusively on green algae and eel grass, *Zostera marina*. It is suggested that the dietary differences may influence its size as well as its color, and that an adequate winter food supply is an important factor.

A. vaccaria appears to feed exclusively on the brown alga, *Egregia*.

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Littoral Sedimentary Processes on Kauai, A Subtropical High Island¹

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ABSTRACT: Beach and shallow water sand samples from the island of Kauai, Hawaiian Islands, were studied to ascertain the effects of climate on the supply of sediment, and of wave action on the dispersal and transport of sand along the shores of this circular island. The littoral sediments of the island are made up of two components: biogenous material, such as shell, coral, and foraminiferal sands, formed near the shoreline; and terrigenous material, consisting mostly of volcanic mineral and rock fragments brought to the beach by rivers.

The northeast trade winds play a dominant part in the climatic and oceanographic processes affecting the island. On the windward side of Kauai, the annual rainfall ranges from 30 inches near the coast to over 460 inches at higher elevations; on the leeward side, annual rainfall is less than 20 inches. This large variation in rainfall results in a climatic range from tropic-humid to semi-arid. Rivers draining the wet, windward portion of the island carry relatively little sand, and the shoreline on this side is characterized by intermittent fringing reefs and beaches of calcareous sand. A detailed study of several reefs on the windward side of the island shows that each pair of fringing reefs, divided by a relatively deep inlet, constitute separate cells for the circulation of water and distribution of sediments.

The highest concentrations of volcanic sand occur on the lee side of the island, where streams draining the semi-arid region enter the coast. The concentration of volcanic material in the beach sands decreases logarithmically with distance along the coast from the rivers.

KAUAI is the next to westernmost of the windward islands of the Hawaiian Archipelago (Fig. 1). It is roughly circular in shape, with a diameter of about 25 nautical miles (Fig. 2). The island is volcanic and has a central plateau whose eastern rim exceeds 5,000 ft in elevation. This mile-high rim intercepts the trade winds, causing moderate to extreme precipitation on the windward slope and producing a rain-shadow desert along portions of the leeward coast.

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The contrast between windward and leeward sides of the island in terms of climate and source of sediment suggested that this island was an ideal locality to study the relation between nearshore sedimentation and the source and type of sediment. It was found that the windward streams, although high in runoff, contributed very little sand-size material to the nearshore areas. On this side, the coastal environment is characterized by fringing coral reefs, with protected beaches composed of calcareous sand derived from shells, reef detritus, and foraminifera. Kapaa Reef had been investigated by Kohn and Helfrich (1957) and, since it seemed typical of the windward reefs, it was selected for more detailed study.

Consistently high concentrations of terrigenous material were found on only a few of the leeward beaches. These deposits were particularly conspicuous near the mouth of the Wai-

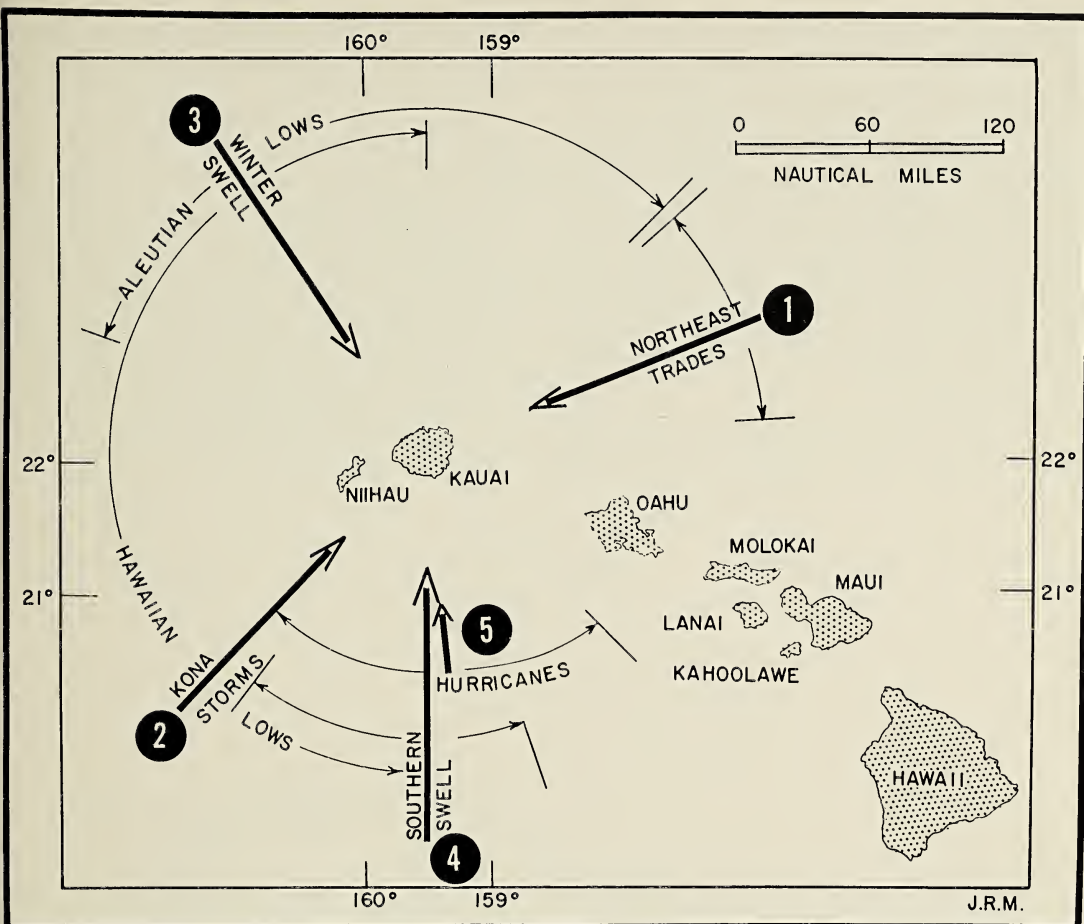


FIG. 1. Index chart and exposure to waves and winds. Heavy arrows indicate directions of approach of the five major wave types which affect the island.

mea River, which drains the major canyon on the island and is in an area of relatively light rainfall. The most typical of the lee beaches investigated lay along the shores of the Mana Coastal Plain.

During the study, it was observed that beach and dune rock is especially well developed along portions of the Kauai coast. This was the subject of a special investigation by Emery and Cox (1956). Some additional observations are discussed under the section on sediments.

PHYSIOGRAPHY

Kauai is one of a chain of volcanic islands in the Hawaiian Archipelago. It formed as a shield volcano built up from the deep floor of the Pa-

cific Ocean by thin flows of basaltic lava. The original shield collapsed to form a broad caldera, which subsequently filled with thicker lava flows and talus deposits. The caldera is now almost obscured by faulting, extensive erosion, and stream cutting. Ninety % of the flows are composed of normal olivine basalt, while the remaining rock is a basalt either very rich (picrite-basalt) or very poor in olivine. A comprehensive and up-to-date review of the geology of Kauai is given by Macdonald, Davis, and Cox (1960).

The ocean floor around Kauai is characterized by a number of sloping terraces which are terminated on their seaward side by a marked increase in slope. Although the depths of the breaks in slopes at the outer edges of the ter-

ences range on various sides of the island from 30 ft to 500 ft, their grouping suggests that terracing occurred at about four separate levels. The shoalest and widest terrace commonly extends to depths of 40 to 90 ft; others extend from about 150 ft to between 240 to 350 ft; and for the deepest, to about 450 ft. The latter depth presumably marks the outer edge of a wave-cut terrace formed during a still stand near the lowest Wisconsin Sea Level. Generally, the 450-ft contour ranges from 1 to 2 miles from shore, although it extends to 4 miles off the west coast.

The most gently sloping part of the insular shelf, that part shoaler than 90 ft, is frequently

characterized by many apparently closed depressions, generally ranging from 10 to 30 ft deep. These are most common on the north coast, although a very large depression occurs on the west coast off Makaha Point (Fig. 2). The configuration of the submarine ridge surrounding this depression suggests that it may be a relic coastal sand dune, formed at a lower stand of the sea, or possibly a relic barrier beach or reef.⁴

⁴ Observations made while diving on this reef during September 1962 subsequent to submission of this manuscript show the reef to consist of a framework of coral. It is believed that it represents a barrier reef formed during a previous lower stand of sea, and the name "Kaheko" is proposed for the reef because of its presumed great age.

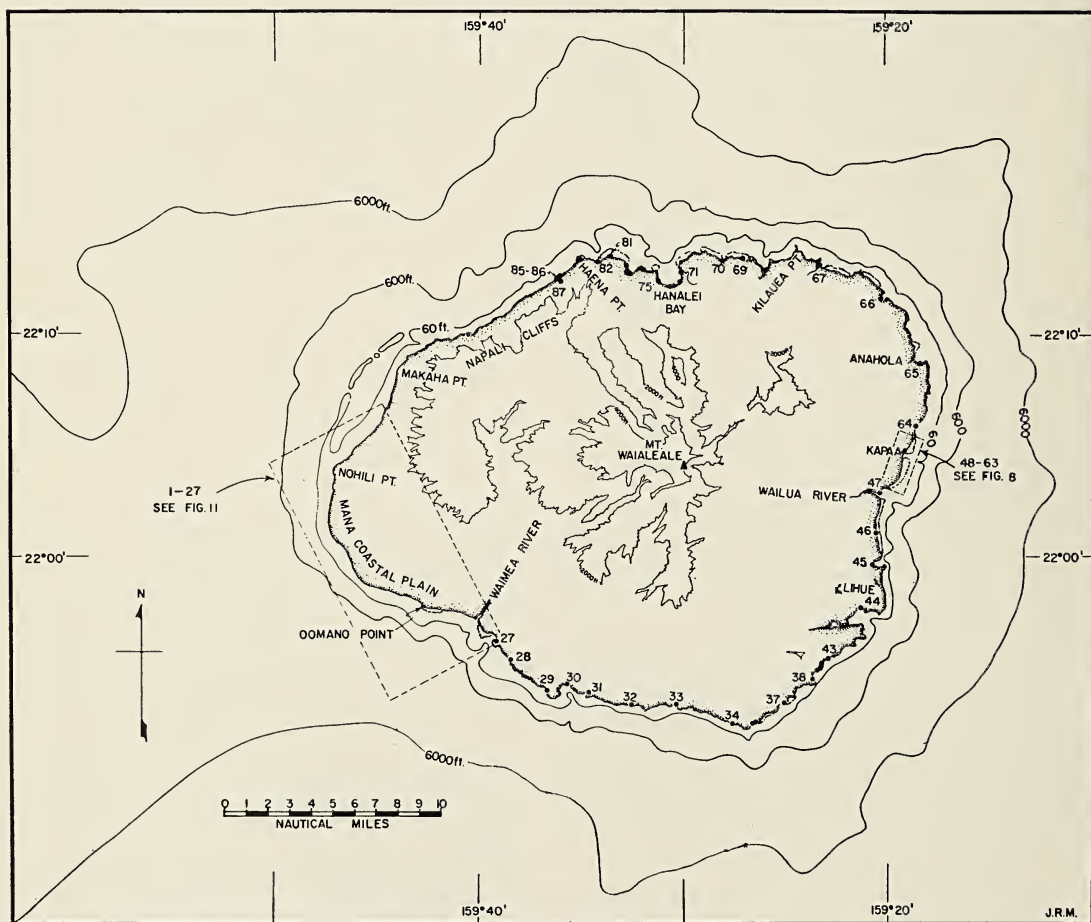


FIG. 2. Topography, bathymetry, and sample locations. Numbers along coastline refer to sample designations listed in text and in Table 2. Intermittent jagged line along shore shows location of major reefs.

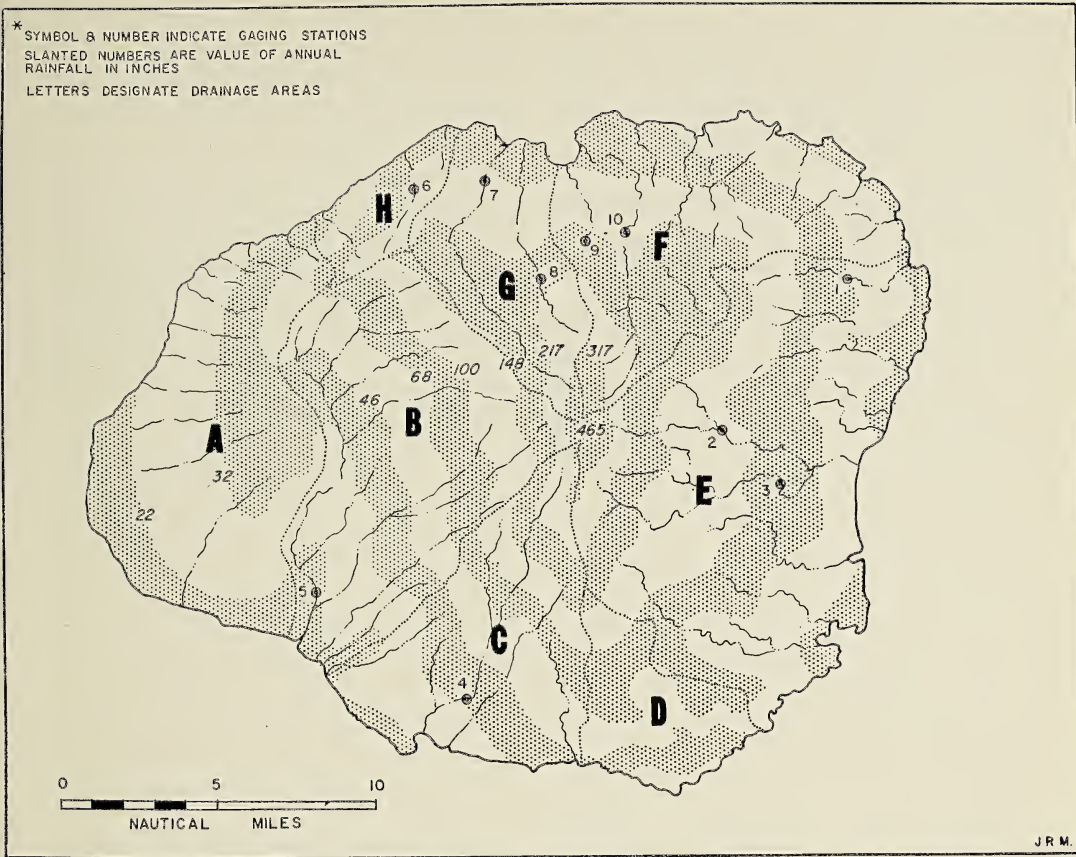


FIG. 3. Rainfall and drainage basins on Kauai. Dotted lines indicate outline of drainage areas. Numbers and letters, designating stream gaging stations and drainage areas, respectively, are referred to in Table 1. Note area of lowest rainfall along western coast. Isohyet lines from the Meteorology Department, Pineapple Research Institute, and the Experiment Station, Hawaiian Sugar Planters' Association, 1948.

There are at least five well-developed sea valleys which cut the shallower portions of the insular shelf. All of these, except the one off Hanalei Bay, appear to terminate above the 450-ft contour.

CLIMATE

The annual precipitation varies from an average of about 50 inches, on the windward (northeastern) shore, to over 450 inches, at the summit of Mt. Waialeale, and decreases to less than 20 inches in the rain-shadow produced on the extreme lee side of the island. Vegetation varies from tropical rain forest on the windward side, to arid on the southwestern slopes. Figure 3 shows the drainage pattern, the outlines of

the major drainage basins, and the contour lines of mean annual rainfall, or isohyets, for the island, as well as the location of several stream-flow gaging stations.

Langbein and Schumm (1958) have shown that the sediment yield from a drainage basin varies as a function of climate, and that the maximum yield occurs for an effective precipitation⁵ of about 12 inches. The effective precipitation⁵ is obtained from the actual precipitation by correcting for evapotranspiration losses to a standard temperature of 50 F. Sediment yield is less for precipitation either greater or less than

⁵ Langbein and Schumm (1958) define "effective precipitation" as the amount of precipitation that would be required at a mean temperature of 50 F to produce the actual annual runoff from the basin.

this optimum value of about 12 inches (Fig. 4). Although sediment yield is influenced by vegetation, temperature, rainfall characteristics, and topography, a rough approximation for sediment yield can be obtained from the effective precipitation.

Data indicative of the differences between the climates of the various drainage basins on Kauai and of the supplies of sediments in those basins are given in Table 1. These data include: (1) a rough calculation of the mean annual rainfall for the various drainage areas; (2) effective precipitation calculated from rainfall; (3) runoff data for the upper portion of some of the drainage basins, obtained from gaging stations; and (4) the percentage of carbonate in the beach sand sample taken nearest the stream mouths.

In general, the table confirms that the greatest precipitation and the most runoff occur on the windward side of the island where the least amount of terrigenous sediment is found in the beach sand. The Langbein and Schumm curve (Fig. 4) shows that the potential sediment yield is appreciably higher when the effective precipitation does not exceed about 35 inches, with a maximum yield corresponding to a value of about 12 inches. The equivalent values in terms of annual rainfall on Kauai⁶ give the band of high sediment yield as occurring where the mean annual rainfall does not exceed 46 inches, and

⁶ After correcting for evapotranspiration, following Langbein et al. (1949: fig. 2).

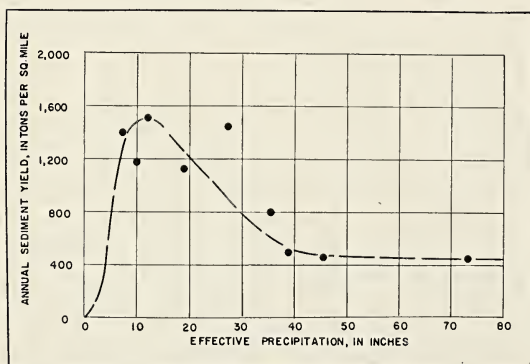


FIG. 4. Relation between effective precipitation and annual sediment yield (taken from Langbein and Schumm, 1958: fig. 3).

a maximum sediment yield corresponding to a mean annual rainfall of 22 inches. Figure 3 shows that a relatively high percentage of the drainage basins on the lee side of the island fall within the range of high sediment yield, whereas the rainfall in the windward drainage basins is appreciably greater and thus produces a somewhat lower yield of sediment. The mean annual rainfall for each drainage basin and the corresponding value for the mean effective precipitation are listed in Table 1, columns 4 and 5, respectively. The Waimea River drainage basin (Fig. 3, B), which is the principal basin on the lee side of the island, has mean values of annual rainfall and effective precipitation of 70 inches and 53 inches, respectively, which are much nearer the value of maximum sediment yield than are those for the principal windward drainage basins (Fig. 3, E, F, G). In fact, much of the Waimea drainage basin falls within the rainfall range of potentially high sediment yield. Also, the sediment yield in the Waimea basin is accentuated by the occurrence of extreme topographic relief in the low rainfall area. This combination of factors, tending to increase sediment yield, does not occur extensively in the windward basins.

The high carbonate content of the beach sand samples on the windward coast tends to confirm the difference in sediment yield between the lee and windward drainage basins (Table 1, last column). In addition, cursory inspection of river banks and river mouths indicated that not only is the yield greater on the leeward side but also that there is a significant difference in the size of the sediment: the leeward streams carry large amounts of sand-size material, whereas the windward streams carry silt and clay-size material. A predominance of silt and clay-size sediment indicates chemical weathering, a process which is enhanced in the windward basins by greater vegetation density and slower rate of removal of disintegration products.

EXPOSURE TO WAVES

Although no complete statistical wave data for spectrums and directions of waves are available for the island of Kauai, a general description of the prevailing wave conditions can be

TABLE 1
RAINFALL, RUNOFF, AND SEDIMENT COMPOSITION FOR DRAINAGE BASINS ON KAUAI

DRAINAGE BASIN					RIVER BASIN ABOVE GAGING STATION					BEACH SAND SAMPLE NEAREST RIVER	
Designation*	Area (sq statute miles)	Mean Annual Temp.† (°F)	Mean Annual Rainfall (inches)	Effective Precipitation‡ (inches)	Designation*	River	Drainage Area (sq statute miles)	Runoff§ (inches)	Maximum Inst. Flow (cubic ft/ sec)	No.	% Carbonate
A	86	70	30	18							
B	96	69	70	53	5	Waimea	45.0	45.0	372	24	1.3
C	64	69	76	55	4	Hanapepe	20.5	52.1	487	30	4.2
D	27	70	67	50							
E	144	67	128	100	3	S. Wailua	22.4	81.0	265	47	80.0
					2	N. Wailua	14.6	99.8	2045	47	80.0
					1	Anahola	5.5	53.5	1010	65	90.0
F	78	69	134	101	10	Hanalei	19.2	196.0	1130	71	62.0
					9	Waioli	1.6	277.0	930	74	76.0
G	40	67	169	130	8	Lumahai	7.1	230.0	1090	76	62.0
					7	Wainiha	14.7	91.9	211	78	55.0
H	14	67	93	70	6	Hanakapiai	2.6	102.0	1600	85	85.0

* Refers to Figure 3.
† Adjusted for mean elevation of basin, assuming 3 F. decrease per 1000 ft altitude. Station temperature from Macdonald, Davis, and Cox (1960: 114).
‡ Precipitation at a mean temperature of 50 F. required to produce the actual runoff. Runoff obtained from mean annual rainfall (extrapolation from Langbein et al., 1949: fig. 2); effective precipitation obtained from annual runoff (Langbein and Schumm, 1958: fig. 1).
§ Annual river discharge divided by the drainage area. River discharge from Territorial Planning Board (1939).

obtained by generalizing from the wave summary given by the Corps of Engineers (1955: appendix B) and from specific storm descriptions, such as that of Arthur (1948). Review of these data suggests that the wave and wind regime can conveniently be classed in the following manner (Fig. 1):

- 1. *Northeast Trades*: Swell generated by the prevailing northeasterly winds. These waves are present all year, but are largest from April through November. Waves typically have periods of 5–8 sec, are 4–12 ft in height, and approach from the east-northeast.
- 2. *Kona Storms*: Waves generated by intense winds, associated with local fronts or Hawaiian lows of extra-tropical origin. The wind may vary in direction from south through west to north, and usually blows hardest from the south-

- west. These storms are not frequent, but occur most commonly from November through March. Waves accompanying these storms typically have periods of 8–10 sec, are 10–15 ft high, and are most intense from the southwest.
- 3. *Winter Swell from Aleutian and Mid-latitude Lows*: Waves from this source are intermittent, and can occur throughout the year, but are most intense from October through May. Typical waves have periods of 10–17 sec, are 8–14 ft high, and may approach from the northwest, north, and northeast.
- 4. *Southern Swell*: Long, low waves generated by storms in the southern hemisphere, and most prevalent from June through September. Typical waves have periods of 14–22 sec, are 1–4 ft high, and approach from the southeast through the southwest.

5. *Hurricane*: Waves from tropical storms, usually approaching from the southeast through southwest. They are most likely to occur in August and September, although occurrence may be between June and December.

Of the five classes of waves, those generated by the northeast trades are by far the most persistent source of wave energy for the east and northeast shores of the island. Undoubtedly these waves account for the greater abundance of calcareous reefs on the windward side of the island. Waves from Aleutian lows are probably the dominant agent responsible for recent erosion along the Napali Cliffs on the northwest coast of the island. These waves produce a southwesterly drift of littoral sediment from the Napali Cliffs towards Nohili Point and have been a major influence in the formation of the straight coast line near Barking Sands (between sample stations 1 to 7, Fig. 11). The meteorological conditions giving rise to unusually high waves of this type in January 1947 are described by Arthur (1948). Waves of this type, with breakers estimated to be 20 ft high and periods of 14–16 sec, were observed on the north coast of Kauai on 30 November 1955.

Southern swell is the most common type of wave on the south and lee sides of the island. Although these waves are low, they are almost continuous during the summer months and produce a westerly transport of sand from the Waimea River toward the Mana Coastal Plain. Hurricanes, although infrequent, are important, and the local residents attribute some recent erosion to the combined effects of the hurricane of 1957 and the tsunami of the same year. Kauai is exposed to tsunami waves accompanying seismic activity in the vicinity of the Aleutian and Kurile Trenches in the northern hemisphere, and, to a lesser degree, from tsunami waves generated off the coast of Chile in the southern hemisphere. These catastrophic waves cause considerable coastal erosion and, at times, transport large blocks of reef material inland (Shepard, Macdonald, and Cox, 1950).

SEDIMENTS

Eighty-three sand samples and five beach and dune rock samples were collected from the near-shore zone along the coasts of the island. Exami-

nation of the sediment showed that it could easily be divided on the basis of origin into: (1) biogenous material derived from the skeletons of molluscs, coral, calcareous algae, and foraminifera; and (2) terrigenous material derived from erosion of the island's volcanic formations. These two sediment types were characterized by important differences in color, density, and solubility in dilute hydrochloric acid. In general, the biogenous material appeared to constitute the predominant sediment in the nearshore region of the island. On the windward coast, the percentage of biogenous material was so high that the terrigenous fraction was rarely visible to the unaided eye.

Most samples were composed of medium and coarse grain sand containing 80% to 95% calcium carbonate of biogenous origin. Analysis by X-ray diffraction showed that, mineralogically, the biogenous material was composed of three components: aragonite, magnesium-rich calcite, and magnesium-poor calcite. Terrigenous sediments were common only on the lee coasts of the island, especially in the vicinity of and down current from river mouths. The terrigenous material consisted mainly of olivine grains and sand-size, partially-weathered feldspathic rock fragments, plus a small percentage of opaque iron oxides.

A brief description of the size distributions of the sands follows, together with their biological, chemical, and mineralogical analyses. Detailed data on each sample are listed in Table 2.

Size Distribution

The size distributions of all the sediments were determined by the Emery settling tube (Poole et al., 1951); and some, especially the coarsest, were also analyzed by sieving. The median diameter of the particle size distribution is expressed in microns, and measures of the standard deviation (sorting) and skewness are given in the graphic phi notation of Inman (1952). Sieving was necessary in order to obtain the parameters for the coarser samples. Since sieve and settling tube analyses are based on different properties of the sediment, the parameters obtained by the two methods are only roughly comparable. For example, the partly hollow tests of foraminifera are retained in a

TABLE 2
LOCATION, TYPE, SIZE DISTRIBUTION, AND COMPOSITION OF SAMPLES

SAMPLE NUMBER	LOCATION	TYPE SAMPLE*	BEACH SLOPE, TANGENT	SIZE DISTRIBUTION†			% CARBONATE‡	CARBONATE FRACTIONS§			OLIVINE TO FELDSPAR PEAK HEIGHT RATIO§
				Median Microns	σ_ϕ	α_ϕ		% Aragonite	% Mg-Rich Calcite	% Mg-Poor Calcite	
1	Barking Sands	B	.067	253 (227)	.31 (.310)	.0 (.0)	72.8	41	59	trace	~.5
2	Barking Sands	B	.101	309 (297)	.39 (.385)	-.08 (-.026)	76.0				
3	Barking Sands	D		451 (435)	.48 (.465)	-.02 (+.043)	82.7				
4	Barking Sands	B	.14	473 (451)	.58 (.50)	-.02 (-.18)	74.8				
5	Barking Sands	B		651 (637)	.48 (.65)	-.25 (.0)	86.8				
6	Barking Sands	BR		beach rock			85.4	27	73	trace	
7	Nohili Point	B	.085	707 (646)	.61 (.48)	+.02 (-.01)	85.0				
8	Mana	B		779 (747)	.45 (.42)	+.02 (-.01)	89.6	28.7	62.8	8.5	
9	Mana	B		245 (243)	.56 (.72)	-.34 (-.42)	88.8				
10	Mana	B		243 (230)	.38 (.46)	-.24 (-.21)	87.3				
11	Kokole	B	.13	281 (330)	.51 (.51)	-.27 (-.20)	88.1				
12	Kekaha	B	.101	257 (262)	.56 (.64)	-.26 (-.12)	86.3				
13	Kekaha	B	.096	262 (257)	.51 (.55)	-.31 (-.08)	86.1	39	61	trace	~.3
14	Kekaha	B	.13	297 (337)	.48 (.49)	-.23 (0.00)	76.9				

TABLE 2 (continued)
LOCATION, TYPE, SIZE DISTRIBUTION, AND COMPOSITION OF SAMPLES

SAMPLE NUMBER	LOCATION	TYPE SAMPLE *	BEACH SLOPE, TANGENT	SIZE DISTRIBUTION†			% CARBONATE‡	CARBONATE FRACTION§			OLIVINE TO FELDSPAR PEAK HEIGHT RATIO§
				Median Microns	σ_ϕ	α_ϕ		% Aragonite	% Mg-Rich Calcite	% Mg-Poor Calcite	
15	Kekaha	B		429 (412)	.46 (.42)	— .13 (+ .10)	52.9	29	71		< .05
16	Kekaha	B1	.19	574 (555)	.69 (.40)	— .05 (+ .05)	34.9				
17	Oomano	B		398 (401)	.49 (.30)	— .29 (— .25)	32.0				< .05
18	Oomano	BR		beach rock			44.8	17	83		< .07
19	Waimea	B	.13	382 (409)	.68 (.44)	— .36 (— .70)	18.8				
20	Waimea	B		240 (200)	.43 (.47)	— .21 (— .12)	7.7				
21	Waimea	B	.11	277 (276)	.53 (.57)	+ .05 (+ .08)	14.7				
22	Waimea	B	.13	335 (274)	.69 (.67)	— .13 (0.00)	4.4				
23	Waimea	B	.12	304 (344)	.62 (.59)	— .25 (+ .14)	6.9				
24	Waimea	B	.13	390 (319)	.81 (.65)	— .21 (— .05)	1.3				.69
25	Waimea	B	.16	293 (304)	.50 (.50)	— .10 (— .06)	00.5				
26	Waimea	S		470 (335)	.63 (.55)	— .16 (— .02)	0.7				
27	Makaweli Landing	B1	.17	330	.38	— .03	84.6	42	58	trace	
28	Koki	B	.17	824	.54	— .02	86.0				
29	Kuunakaiole Park	B1	.17	532	.35	— .11	90.8				

TABLE 2 (continued)
LOCATION, TYPE, SIZE DISTRIBUTION, AND COMPOSITION OF SAMPLES

SAMPLE NUMBER	LOCATION	TYPE SAMPLE *	BEACH SLOPE, TANGENT	SIZE DISTRIBUTION†			% CARBONATE‡	CARBONATE FRACTION§			OLIVINE TO FELDSPAR PEAK HEIGHT RATIO§
				Median Microns	σ_ϕ	α_ϕ		% Aragonite	% Mg-Rich Calcite	% Mg-Poor Calcite	
30	Hanapepe Bay	B2	.17	259	.46	+.04	4.2				
31	Wahiwa Bay	B	.17	321	.48	-.17	52.7	28	52	20.2	<.15
32	Nahunakueu	B	.13	289	.29	-.17	79.7				
33	Lawai Bay	B	.072	182	.32	+.06	80.8				
34	Poipu	B2	.17	277	.58	-.33	88.6				
35	Makahuena	BR		beach rock			91.5	25.8	69.7	4.5	
36	Makahuena	B	.11	285	.34	-.09	89.1				
37	Kapunakea	B	.17	295	.32	-.22	89.0				
38	Kipu Kai	B	.11	222	.30	-.20	89.1				
39	Kipu Kai	B2	.16	196	.28	-.19	86.7				
40	Kipu Kai	DR		dune rock			88.9	trace	0.0	100	
41	Kipu Kai	BR		beach rock			90.8	45	45	10	
42	Kipu Kai	B	.14	518 (543)	.90 (.69)	-.06 (+.07)	87.8				
43	Kipu Kai	B		(1240)	(.35)	(-.06)	91.2	25	75		
44	Nawiliwili	B	.096	162	.63	-.13	87.0				
45	Hanamaulu	B	.085	139	.47	-.06	78.2	33.3	54.4	12.2	
46	Military Reservation	B1	.19	387	.48	-.21	90.0				
47	Wailua	B	.15	342	.40	-.13	80.0				
48	Kapaa	B1	.16	361	.46	-.19	91.1	29.5	50.1	20.4	
49	Kapaa	B1	.18	500	.39	0.0	93.3	36.8	46.7	16.5	
50	Kapaa	O		371	.40	-.02	90.0	33.3	48.0	18.7	
51	Kapaa	B1	.16	420	.57	-.15	92.4	30.0	53.2	16.8	

TABLE 2 (continued)
LOCATION, TYPE, SIZE DISTRIBUTION, AND COMPOSITION OF SAMPLES

SAMPLE NUMBER	LOCATION	TYPE SAMPLE *	BEACH SLOPE, TANGENT	SIZE DISTRIBUTION†			% CARBONATE‡	CARBONATE FRACTION§			OLIVINE TO FELDSPAR PEAK HEIGHT RATIO§
				Median Microns	σ_ϕ	α_ϕ		% Aragonite	% Mg-Rich Calcite	% Mg-Poor Calcite	
52	Kapaa	B1	.16	500	.53	—10	93.3	29.3	52.1	18.6	
53	Kapaa	B1	.19	490	.60	—06	89.7	25.8	57.5	16.7	
54	Kapaa	B2	.19	525	.55	0.0	93.8	27.0	54.9	18.0	
55	Kapaa	B1	.17	555 (651)	.52 (.33)	—06 (+.09)	92.7	26.6	56.5	16.9	
56	Kapaa	RF		785 (901)	.45 (.37)	—33 (—06)	92.7	23.1	53.8	23.1	
57	Kapaa	B1	.16	595	.61	—05	91.3	26.7	57.2	16.1	
58	Kapaa	RF		(599)	(.51)	(—37)	87.9	27.7	53.8	18.5	
59	Kapaa	O		(829)	(.37)	(—19)	90.7	22.2	54.5	23.2	
60	Kapaa	O		785 (801)	.62 (.44)	—11 (—14)	95.0	25.6	54.3	20.1	
61	Kapaa	B1	.19	493	.60	0.0	93.3	29.8	55.4	14.8	
62	Kapaa	B1	.17	669 (807)	.60 (.38)	+23 (+.18)	90.3	27.2	60.4	12.4	
63	Kapaa	RF		(959)	(.53)	(—11)	88.2	26.7	62.3	11.0	
64	Kaalia	B	.17	289	.27	—33	88.5				
65	Anahola Bay	B	.17	335	.46	—30	89.7				
66	Molooa Bay	B	.12	603	.60	—13	88.9				
67	Kilauea Bay	B		254	.42	—07	75.9				
68	Kalihiwai Bay	B	.14	242	.36	—33	71.8				
69	Kalihikiai	B1	.13	149	.34	—09	88.0	19	81	trace	
70	Anini	B		369	.97	—19	85.4	46	54	00.0	
71	Hanalei Bay	B	.11	172	.34	—29	62.0	52	48	trace	<.2
72	Hanalei Bay	B	.037	190	.39	—13	48.9				

TABLE 2 (continued)
LOCATION, TYPE, SIZE DISTRIBUTION, AND COMPOSITION OF SAMPLES

SAMPLE NUMBER	LOCATION	TYPE SAMPLE*	BEACH SLOPE, TANGENT	SIZE DISTRIBUTION†			% CARBONATE‡	CARBONITE FRACTION§			OLIVINE TO FELDSPAR PEAK HEIGHT RATIO§
				Median Microns	σ_ϕ	α_ϕ		% Aragonite	% Mg-Rich Calcite	% Mg-Poor Calcite	
73	Hanalei Bay	B	.101	341	.51	—20	74.2				<.2
74	Hanalei Bay	B		330	.55	—04	76.2				
75	Hanalei Bay	B	.13	364	.54	—11	67.4				
76	Lumahai Bay	B	.18	611	.71	—14	62.5	29	71	trace	.2
77	Lumahai Bay	B, BC		475	.56	—18	10.7				3.9
78	Wainiha Bay	B	.16	(1347)	(.27)	(—07)	54.6	25	75	0	<.06
79	Wainiha Bay	B, BC		369	.55	—22	11.7				2.7
80	Wainiha Bay	B	.19	717	.43	+14	92.5				
81	Haena Point	B1	.19	871	.39	+32	90.7				
82	Haena	B	.16	819 (707)	(.64)	(—09)	89.1				
83	Ke'e	B1	.20	369 (309)	.38 (.35)	—18 (0.00)	6.8				
84c	Ke'e	RF		344	.62	—40	64.4				
84t	Ke'e	RF		295	.66	—50	53.0				
85	Hanakapi'ai	B		620	.78	+09	85.3				
86	Hanakapi'ai	B	.043	242	.33	—12	23.8				
87	Hanakapi'ai	S		(3732)			0.5				

* Sample type: B, beach sand; B1, beach sand (protected by fringing reef); B2, beach sand (very protected bay); BC, heavy mineral concentrate not typical of whole beach; BR, beach rock; D, dune sand; DR, dune rock; O, offshore sand; S, stream sand; RF, reef sand.
† Size parameters enclosed in parentheses were obtained by sieving; unenclosed values were from analysis in an Emery settling tube. Deviation (sorting) and skewness are in graphic phi measures (Inman, 1952).
‡ Gasometric analysis (Bien, 1952).
§ X-ray diffraction analysis.

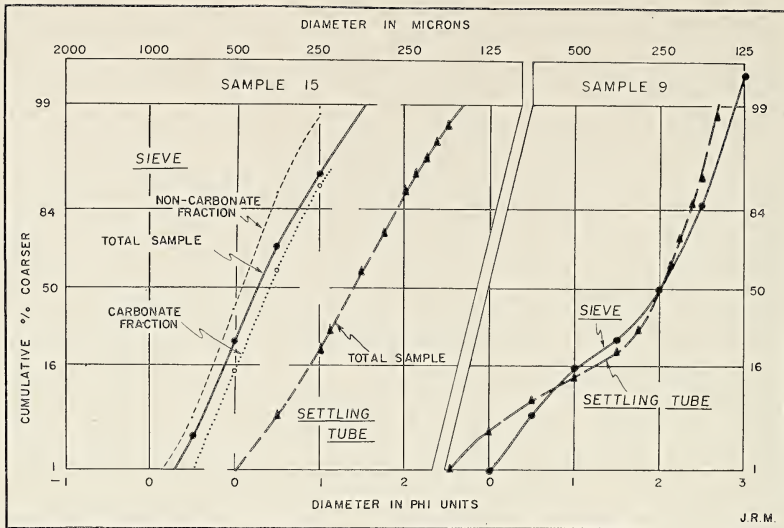


FIG. 5. Size distribution curves for sand samples 9 and 15, showing comparison between settling tube and sieve analysis. Grain size distribution curves are also presented for the carbonate and noncarbonate fractions, which make up 53% and 47%, respectively, of sample 15. The size distribution curves for sample 9 (89% calcium carbonate) show a marked bimodal distribution, which is not typical of most highly calcareous samples of Kauai. In this case, the bimodal distribution reflects the differences between the coarse carbonate grains arriving from the north and the finer, but more abundant, carbonate grains from the east.

coarser sieve fraction than their settling velocity would indicate. Comparisons between sieve and settling tube analyses are shown in Figure 5.

The most common beach sediment had a median diameter of about 350 microns, while the median size of all samples ranged from 140 to 1400 microns. Although the size distributions of the samples from the windward and leeward coasts as a group were not markedly different, smaller coastal segments did show significant longshore trends of increasing or decreasing grain size. There is a tendency towards bimodality in sediment size distribution, especially where mixing of sediment from different transport directions occurs southeast of Nohili Point (Sample 9, Fig. 5). Also, the beach face sediments from Kauai, which had an average phi deviation measure of about 0.5, are less well sorted on the average than those from typically continental beaches. Well-sorted sand of similar size from continental beaches would have a phi deviation measure of about 0.3 (Inman, 1949, 1953). The more frequent interruption of littoral drift by points and headlands, and the con-

tinuous addition of a heterogeneous assortment of material from reefs and from offshore, probably account for this difference in sorting.

The slope of the beach face increases with increasing sand size and with decreasing wave height and intensity. Beaches like those at Kapaa, which are protected by broad fringing reefs from the direct attack of large breakers, were consistently steeper than more exposed beaches. Also, beaches inside protected bays (as Station 30, Hanapepe; Table 2) were steeper than those exposed to the open sea (as Stations 1-7 at Nohili, and Station 86 at Hanakapi'ai). The relation between beach slope and sand size for various type beaches is given in Figure 6.

Biological Analysis

The only completely identifiable biogenous components present in significant quantities in the sands were the benthic foraminifera *Heterostegina suborbicularis* and *Amphistegina madagascariensis*. Other positively recognizable components, including other foraminifera, echinoid spines, sponge spicules, gastropod shells and

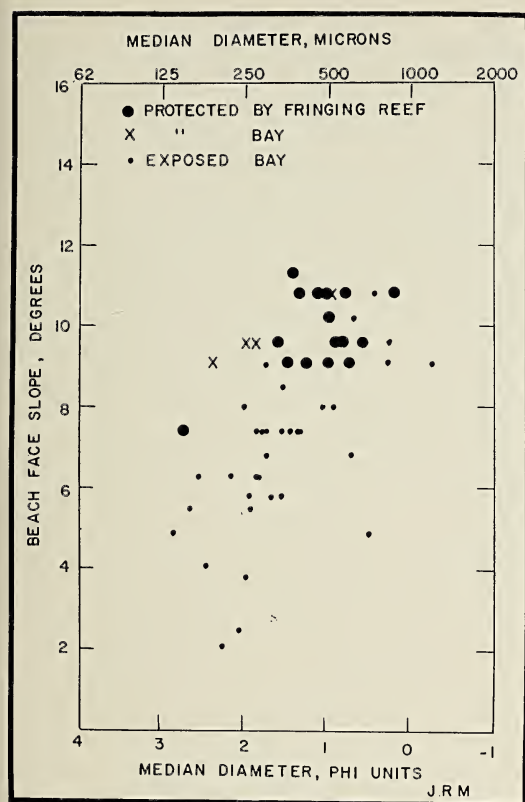


FIG. 6. Relation between beach slope and sand size. Exposed beaches generally have lower slopes than protected beaches.

opercula, pelecypod valves, and bryozoan fragments, made up less than 5% of the samples. Most of the remaining nonterrestrial component of the sand consisted of rounded calcareous grains, sometimes etched, pitted, or stained.

A rough count indicated that *Amphistegina* and *Heterostegina* accounted for up to 20% of the grains in some of the samples. Since these foraminifera occurred most commonly in the size range of 500 to 1500 microns, they were more abundant in the coarser sediments. *Amphistegina* were most common in the finer half of this range.

Several identifiable skeletal or shell fragments, collected from the reefs and beaches of Kauai, or in one case from Oahu, were examined by X-ray diffraction. The results and a review of the literature suggest that, in this area, the aragonite is secreted principally by corals and

molluscs; the magnesium-rich calcite by foraminifera, coralline algae, and echinoids; and the magnesium-poor calcite by molluscs and by *Amphistegina madagascariensis*.

Chemical and Mineralogical Analysis

All of the sand samples were examined qualitatively, and representative samples were also examined quantitatively to determine the chemical, mineralogical, and biological composition. The carbonate content of all of the samples was determined to an accuracy of about 1%, using a gasometric technique described by Bien (1952). Mineralogical determinations were made with a petrographic microscope and by X-ray diffraction, using a North American Phillips Diffractometer.

TOTAL CARBONATE: The total carbonate content varied from 0.5%, in the river bottom samples, to 95% in some beach samples. Fifty-two of the samples had carbonate contents greater than 80%, while only 17 contained less than 50% CaCO_3 . Although high carbonate values occurred on all coasts, samples from the east coast were composed almost entirely of biogenous material. The sands showing the highest carbonate values on the north, south, and Mana coasts were taken from those beaches which were most distant from large streams (Table 2). On the east (windward) coast and on the eastern part of the north coast, the presence of large streams appeared to have little effect on the carbonate content of the beach sediments. Low carbonate values were typical of the beaches west of the Waimea River mouth on the south coast between sample stations 15 and 25 and, to a lesser degree, in Hanalei Bay on the north coast.

CALCITE: The X-ray patterns of the sand samples showed that the calcite frequently consisted of two components, magnesium-rich and magnesium-poor calcite (Fig. 7). A quantitative determination of the amount of magnesium carbonate in each of the calcite components (i.e., the mineral species of the component) was made by comparing the peak location of each component with the curve published by Goldsmith et al. (1955: fig. 1). In the Kauai samples, the magnesium-poor peak represents a calcite containing from 2% to 3% MgCO_3 ; the magnesium-rich peak represents a calcite containing

about 13% MgCO_3 . Determination of the amount of both of the calcite components, and of the aragonite component in the carbonate fraction of each sample, was made by comparing the peak ratios of these components prepared from known mixtures of the components (Gayman, in preparation; Lowenstam, 1954). Although recognized corrections have not been made, it is thought that the relative quantitative results are significant.

In all of the samples examined, with the exception of one dune rock sample (40), the magnesium-rich calcite was much more abundant than the magnesium-poor calcite. This rock was obtained from a lithified relic dune which now forms a headland (sample station 40) of Kipu Kai Valley, south of Lihue. With this one exception, magnesium-poor calcite never constituted more than 25% of the carbonate content of any sample.

Magnesium-rich calcite was always present in the unconsolidated samples, and it was fre-

quently the only calcite component found. Magnesium-poor calcite was absent from the north and Napali coasts, and was abundant only in the dune rock and on the east coast in the vicinity of Kapaa Reef. The distribution of magnesium-poor calcite in the Kapaa area and the anomalous abundance of this component in the dune rock (sample 40) are discussed subsequently.

According to Chave (1954a), water temperature and phylogenetic level are principle factors in determining the magnesium content of biogenous calcite. High magnesium content is favored by warmer water and lower phylogenetic level. Temperature has less effect on the magnesium content of the higher phylogenetic levels. Blackman and Todd (1959) show magnesium content in foraminifera to vary with family. *Heterostegina*, one of the two common species of foraminifera in the samples, and two unidentified species of coralline algae taken from Kapaa Reef, were X-rayed and found to contain only magnesium-rich calcite. Conversely, *Amphistegina*, the other common foraminifera, and a limpet were found to be composed mostly or entirely of magnesium-poor calcite.

ARAGONITE: Aragonite is generally considered to be indicative of warm water deposition. It is deposited by three quantitatively significant groups (Lowenstam, 1954): calcareous algae, scleractinian corals, and molluscs. Samples from Kapaa Reef of two different species of coral (*Acropora* and a scleractinian coral) and one specimen of gastropod (*Conus*) were X-rayed and found to be pure aragonite. One limpet, mentioned previously, was found to be predominantly magnesium-poor calcite and only 28% aragonite. Although the aragonite in the carbonate fraction ranged from 19% to 45%, no systematic variation with depth or direction was apparent.

TERRIGENOUS: A cursory inspection of the differences in the terrigenous mineralogy was made by microscopic and X-ray diffraction techniques. A limited amount of X-ray data on the terrigenous components of the samples is presented in Table 2 in the form of the olivine to feldspar peak height ratios. These data should be regarded as only semiquantitative because of the variation in peak height introduced by preferred orientation of the feldspar crystals.

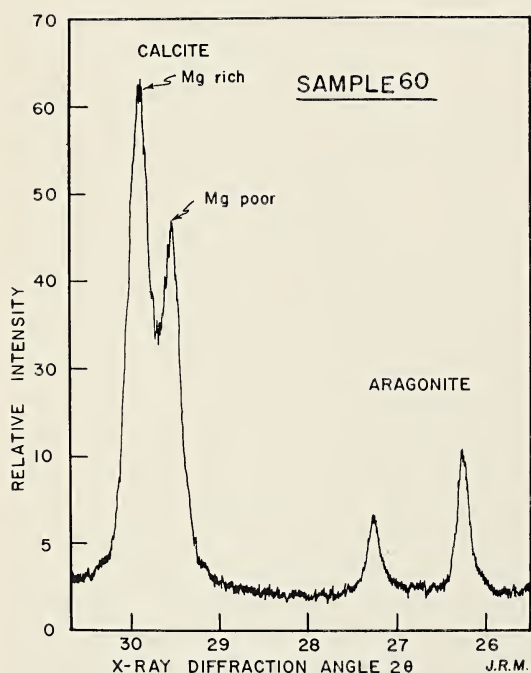


FIG. 7. X-ray diffraction analysis of sample 60, showing the magnesium-rich and magnesium-poor peaks and the two aragonite peaks. The sample was taken in a water depth of 27 ft outside of Kapaa Reef (Fig. 8).

Presumably, a difference in the degree of chemical weathering accounts for the differences in mineralogy between the terrigenous sediments on the windward and leeward coasts. Plagioclase-rich sands occur near the Waimea River mouth, while on the north coast the same size grades of sand are plagioclase-poor and olivine-rich; however, there appears to be little difference in the average parent rock in the two source areas. It seems likely that a more rapid decomposition of feldspar, relative to olivine, takes place because the feldspar occurs in smaller mineral grains. The plagioclase crystals, found only in sand-size rock fragments, are several orders of magnitude smaller than the olivine grains found in the beach sands. The plagioclase crystals are abundant in medium- and fine-grain beach sands only in the Waimea area. Apparently the easily decomposable volcanic rock fragments in these size ranges are brought to the shore in mass only where chemical processes are at a minimum. On Kauai a maximum in sediment yield and a minimum in chemical weathering occur only in the arid Waimea drainage basin.

Beach and Dune Rock

The distribution of beach rock on Kauai is described by Emery and Cox (1956) in a comprehensive study of beach rock in the Hawaiian Islands. They examined 72 miles of sandy beaches on Kauai and reported beach rock along 21 miles, or about 13% of the entire coastline. The total occurrence of beach rock may be even greater, as the presence of beach rock is frequently obscured by a covering of loose clastic sand. During the present study, a large outcrop of beach rock that was surveyed and sampled (No. 18) at Oomana Point in 1955, was completely covered with fresh sand when the site was revisited in 1959. Also, in the vicinity of samples 38 and 39, it was found that a $\frac{1}{4}$ -mile section of beach rock was covered with a uniform layer of fresh sand, about 4 inches thick. Here the slope and general attitude of the beach rock was the same as that of the fresh beach face. Water seeping through the beach face was tasted and found to be fresh, indicating that its origin was the fresh water ponded behind the beach ridge.

In fact, there is some correlation on the island of Kauai between beach rock outcrops and areas of present or past ponding of fresh water behind calcareous beach ridges. Although it is recognized (Emery and Cox, 1956) that there may be several methods of formation of beach rock, it appears that an important cementation process on Kauai is associated with the evaporation of fresh calcium carbonate-rich waters seeping through the beach face. This occurs most generally when fresh water is ponded in calcareous sediments by sand dunes or beach ridges. Presumably, the fresh or brackish water flowing through the porous calcareous sediments becomes saturated with CaCO_3 . Evaporation of this water on or near the beach face causes cementation, and rock is formed if the beach is sufficiently stable. This belief is strengthened by the presence of cemented dune sands, which are well above sea level and appear to have been formed in the same manner as the beach rock, with which these cemented sands are commonly associated.

Dune rock (eolianite) was found on the southwest coast of the island, northeast of Nohili Point. Near Nohili the dune rock was poorly cemented and appeared to be contemporaneous with the formation of the present dunes at Barkling Sands. In the vicinity of Kipu Kai (sample 40) several rocky points, such as Alligator Head, are composed of well-cemented dune rock, which is now exposed to wave attack. The Kipu Kai dune rock is older than the present shoreline.

Thin section studies of beach and dune rock samples (6, 18, 35, 40, 41) confirm the lithologic and biologic similarity of the rock samples and the recent beach sand. The general structure, texture, and composition of the beach rocks suggest that they were formed either very recently, or under the same environmental conditions as those which are now dominant on Kauai beaches. Examination of thin sections and X-ray analysis suggest that the cement is calcitic, in agreement with the findings of Emery and Cox (1956).

The only dune rock sample, 40, differed from the beach and beach rock samples in that the carbonate fraction is composed entirely of magnesium-poor calcite and the cement was considerably more abundant. It does not seem likely that the single carbonate mineral species now found

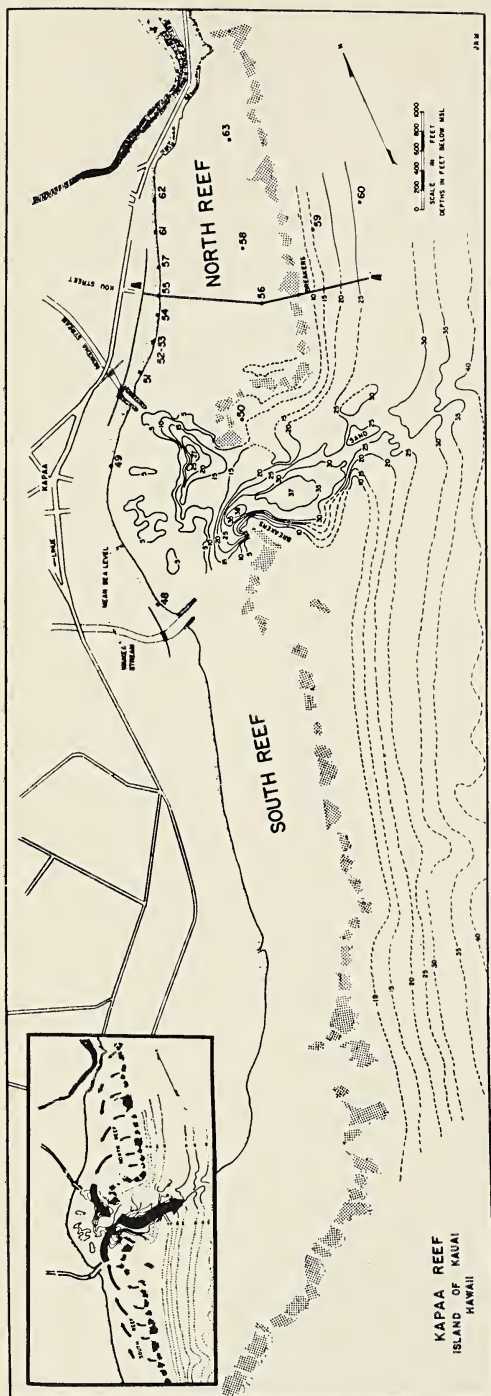


FIG. 8. Bathymetry and sample locations along Kapaa Reef. Dotted areas depict breaker zone on outer edge of reef platform. The circulation pattern of wave generated currents over the reef is shown in the inset. (Bathymetry compiled from Board of Harbor Com-

missioners Survey of 1919; photomosaic by R. M. Towell Inc., 1950; and miscellaneous soundings in 1957 (?) by H. V. Frasier, Hawaiian Dredging Co., and in 1959 by Sam Keala, Jr., of Lihue Plantation).

in the rock results from a monomineralic species in the biogenous material of the original deposit. The presence of the single carbonate mineral species may be most easily accounted for by assuming (1) the inversion of an original aragonite component to calcite (see Jamieson, 1953); and (2) alteration of magnesium-rich to magnesium-poor calcite by the diagenetic loss of magnesium ions from an original magnesium-rich calcite component (see Chave, 1954b). The time required for such processes to be carried to completion, and the present physiographic position of this fossil dune, both suggest that it is considerably older than the neighboring beach rock.

KAPAA—A WINDWARD REEF AND BEACH

Kapaa Reef lies along the windward east coast of Kauai, and has an overall length of about $2\frac{1}{2}$ miles along the north-south trending coastline in the vicinity of the town of Kapaa. It is a fringing reef and is divided into northern and southern portions by an inlet through the reef where two small streams enter the ocean near the center of the town. The Kealia River enters the ocean about 1 mile north of Kapaa, and the Wailua River enters the coastal embayment to the south of the reef. Although both rivers have appreciable runoff, they contribute relatively little sand-sized material to the littoral zone.

North Kapaa Reef is approximately 4,000 ft long, and varies in width from about 400 ft at its northern end to 1,500 ft at the southern end, where it is terminated by the inlet (Fig. 8). The reef platform has an average depth of about $2\frac{1}{2}$ ft below mean sea level, and the tide has a diurnal range of 1.8 ft. The inshore edge of the reef is bordered by a beach of medium- to coarse-sized calcareous sand. The beach has an average height of berm above mean sea level of about $6\frac{1}{2}$ ft, and has a total thickness of sand above the reef platform of about 8 ft. A remnant toe of beach rock, which outcrops intermittently on the reef flat 10–40 ft offshore from the present beach (Fig. 9), indicates a slight recession of the beach. The seaward portion of the

missioners Survey of 1919; photomosaic by R. M. Towell Inc., 1950; and miscellaneous soundings in 1957 (?) by H. V. Frasier, Hawaiian Dredging Co., and in 1959 by Sam Keala, Jr., of Lihue Plantation).

reef is shallow, and causes waves to break in all weather. The seaward slope of the reef rises from a depth of about 15 ft, and is made irregular by numerous channels and solution and abrasion cavities (Figs. 9, 10). Beyond the base of the reef, the sea floor has a gentle slope out to the 60-ft deep terrace. This terrace, which is common to the submarine topography of Kauai, occurs about 1 mile offshore in the vicinity of Kapaa. A sea-valley extends from near the inlet between North and South Kapaa Reefs, across the shelf and into deeper water (Figs. 2, 8).

The surface of the reef platform is very irregular and consists of a series of low intermittent channels and ridges (described by Munk and Sargent, 1954) which trend east-west and resemble in miniature the channels on the reef at Bikini Atoll. The channels are most pronounced on the northern and central portions of the reef and, although discontinuous, traverse the reef from the breaker zone to near the beach, where they enter the north-south trending depression which commonly exists at the toe of the beach.

Littoral Processes on the Reef

The circulation pattern of water over North Kapaa Reef is from north to south; over that portion of South Kapaa Reef near the inlet, it

is from south to north (inset, Fig. 8). The currents flowing from the north and south reefs converge on the inlet and result in a seaward flow of several knots through the inlet. The anomalous depths of 27 and 38 ft, found relatively near shore in the inlet channel, are probably maintained free from sand by scour associated with the seaward-flowing current.

Measurements on North Kapaa Reef by Helfrich and Kohn (1957) show that both current velocity and the southerly component of velocity increase to the south. They obtained average values of current of about 1 ft per second on the central portions of the reef and a maximum flow of about 1½ ft per second near the Moikeha Jetty. The most intense southerly flow of water occurs roughly one-third of the way between the beach and the seaward edge of the reef; currents at the toe of the beach were somewhat weaker.

The currents appear to result primarily from the mass transport of water associated with waves breaking over the reef. Winds may also be a factor in driving the currents, but their effect is minor, as evidenced by the prevailing northerly flowing current over portions of South Kapaa Reef. Also, on several occasions, southerly flowing currents were observed flowing over the north reef in opposition to brisk winds blowing from the south.

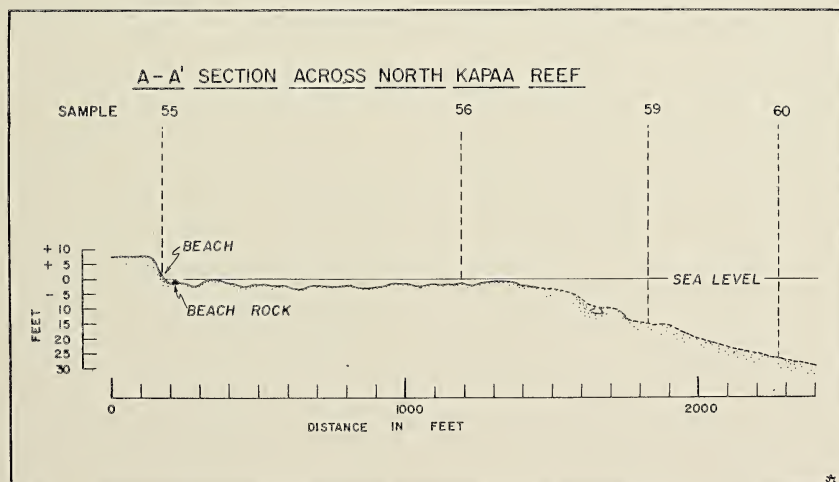


FIG. 9. Section across North Kapaa Reef along line shown on Figure 8. Vertical exaggeration is 10 x. Survey by Sam Keala, Jr., and Hiro Murashige of Lihue Plantation; outer reef and sea floor offshore from the reef based on soundings by authors.

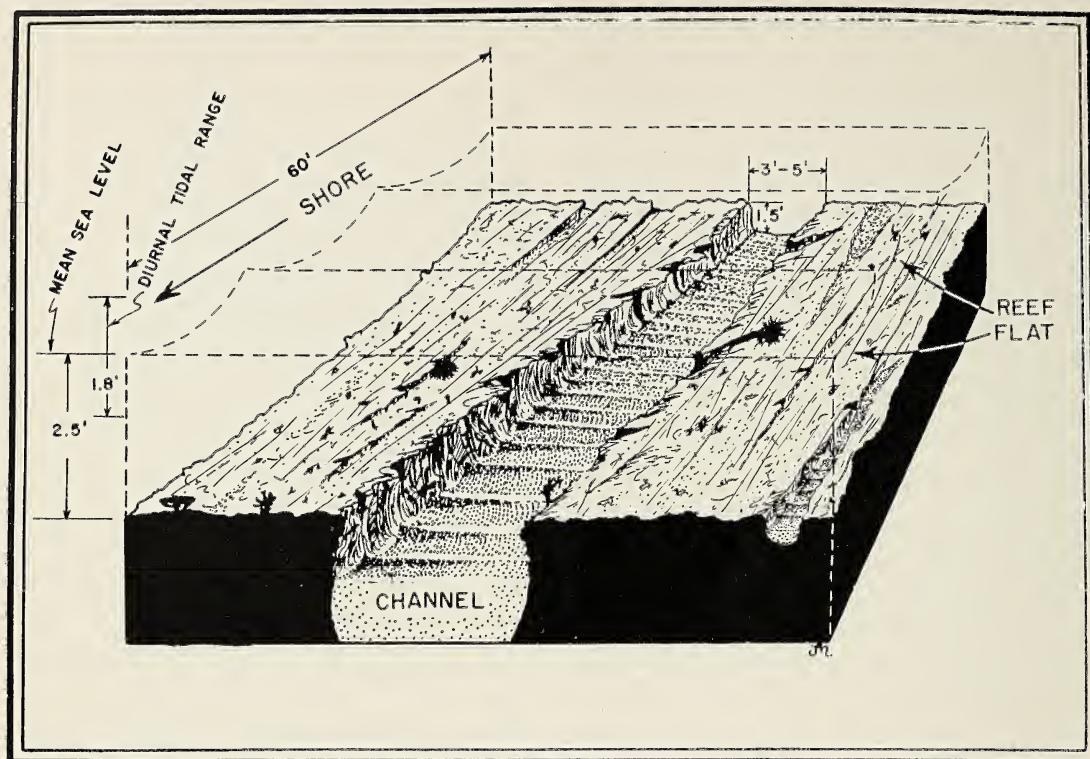


FIG. 10. Generalized sketch of surge channel on Kapaa Reef. Note sediment fill and ripples in bottom of channel. Sand in channels is moved shoreward by the small waves, which reform from the mass of water surging over the reef as larger waves break on outer reef. Prevailing currents, which flow from north to south (to the right of the viewer), are relatively ineffective in transporting sand on the reef flat.

Investigations indicate that the transportation of sand and the circulation of water over Kapaa Reef do not follow the same paths or cycles. While the water circulation is principally from north to south over the north reef, the east-west trending channels, which are common on the reef flat, act as traps for the sand, and prevent any appreciable southerly transport across the reef flat by water currents. The floors of the channels are covered with sand and reef rubble, in some places to a thickness of several feet. The sand is rippled by small waves moving across the reef flat from east to west, resulting in a net transport of sand toward the beach (Fig. 10). These low waves, which move sand across the reef flat, are formed from the mass of water which surges over the reef. The characteristic pattern is for waves of several feet or more in height to break on the outer reef, their momentum carrying a considerable amount of water

over the reef in the form of a surge of white water. Over the reef flat, the surge first forms into a single wave crest, which may, in turn, disperse into a train of several smaller waves as the wave front moves toward the beach. The reef waves thus formed have heights in the neighborhood of $\frac{1}{2}$ to 1 ft, and wavelengths in the order of 20 ft. Water level and shoals on the reef control the height of the waves, for waves higher than the approximate depth of water tend to break and re-form as lower waves. Observations made while swimming over the reef indicate that the small waves are solitary in nature and that their particle or orbital velocity is greater in the onshore than in the offshore direction. This differential between onshore and offshore particle velocity, that accompanies the small waves, results in a step by step movement of sand toward the beach.

The east-west trending channels of the reef

flat appear to play a unique role in the cycle of sand transportation over the reef. They function effectively as traps for sand that might otherwise be transported laterally along the reef by water currents and, at the same time, act as open conduits for the onshore transportation of sand by wave action.

Once on the beach, the sand probably undergoes a slow net southerly drift under the combined action of currents and waves impinging on the beach face. After migrating to the inlet, the sand is carried out to deeper water by the relatively strong currents that flow seaward through the inlet.

Thus, the transportation cycle of sand on the reef appears to include: (a) migration of sand along the channels in the reef flat, which is induced by wave action; (b) southerly transport of sand along the beach face and at the toe of the beach by waves and currents; and (c) seaward transport of sand through the inlet and into deeper water by the currents which converge from the north and south reef and flow seaward.

The sand on the beaches apparently is derived from organisms living on the reef, and from material transported in suspension by waves breaking over the reef. Diving observations indicated that the numerous solution cavities and the general rough outer edges of the reef cause considerable turbulence in the breaking and near-breaking waves. This turbulence increases their capacity for carrying material in suspension. Undoubtedly some reef material also undergoes a net offshore migration by processes of turbulent diffusion. Whether this loss is greater or less than the supply of material to the reef from offshore is not known.

The position and growth of the reef, in recent geologic time, appears to be governed by the combined effects of land runoff and the water circulation and sand transportation over the reef system. Inlets tend to occur in the fringing reefs where streams enter and bring fresh water and mud, which are detrimental to the reef building corals and algae. The reef builders flourish where wave action is most vigorous. Therefore, the reef platform becomes more extensive in the areas not influenced by land runoff. The formation of a wider reef platform causes more and more water and sand to cross the reef and flow into the inlets. The scouring action on the inlets by

water and sand derived from the reef maintains the inlets even when rivers are not flowing. Thus it would appear that once the position of a potential inlet is determined by land runoff and coastal configuration, the pattern of water circulation and sand transportation on the growing reef will tend to perpetuate the location of the inlet.

Kapaa Sediments

Samples collected from the beach, reef flat, and sea floor outside the reef all consisted of very coarse, coarse, and medium-grain sands, containing about 90% calcium carbonate of biogenous origin. The following trends in the sediment were observed from north to south along the north Kapaa reef flat: (1) the sand becomes finer, (2) the sands become better sorted, (3) the magnesium content of the calcite decreases, and (4) the foraminifera content in the sand decreases. In general, the reef flat and offshore samples were coarser than the beach samples. These trends, although not necessarily definitive in themselves, are in agreement with the modes and cycles of sediment transport as discussed previously. The samples from the Kapaa area contained a higher percentage of magnesium-poor calcite than any of the other unconsolidated sediment samples collected from Kauai. In general, the content of magnesium-poor calcite increases southward on Kapaa beach and seaward across the reef. The distribution of magnesium-poor calcite is consistent with the supposition that the supply of beach sand is predominantly from transportation over the reef opposite the beach, rather than from transportation along the shore.

The only completely identifiable biogenous components present in significant quantities in sands were the foraminifera *Heterostegina suborbicularis* and *Amphistegina madagascariensis*. A rough estimate indicated that these species made up 3% to 20% of the grains in the samples. All of the tests were considerably worn, making it quite difficult to separate the two species under a microscope. A more accurate determination of their relative abundance, based on their skeletal composition, was obtained by X-ray diffraction. In sample 59, about 55% of the foraminiferal carbonate consisted of magnesium-rich calcite, indicating deposition by *Het-*

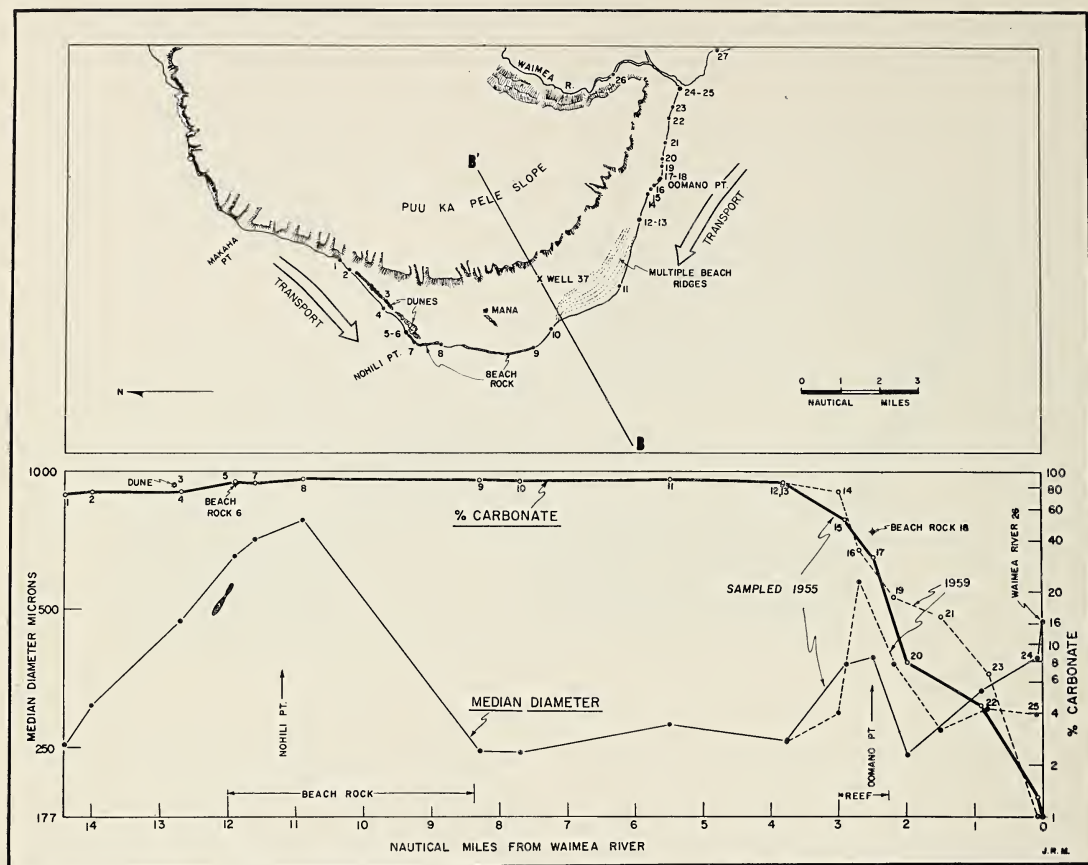


FIG. 11. Top: Direction of littoral transport and sample locations along the Mana Coastal Plain. Note beach rock outcrops, and position of multiple beach ridges and recent and ancient dunes.

Bottom: Variation in carbonate content and median grain size with distance along the Mana shoreline. Median diameters determined by Emery settling tube.

erostegina. The remaining 45% was magnesium-poor calcite and presumably is derived from *Amphistegina*. Very little is known of the living depth range of either species. The highly worn appearance of all of the tests suggest that on Kauai they do not live on the reef but have been transported some distance.⁷

MANA COAST—LEEWARD BEACHES

The Mana Coastal Plain (Fig. 11) consists of calcareous beach, dune, and lagoon sediments, mainly of marine biogenous origin, but including some terrigenous sands near the Waimea

River. Well borings show that these marine sediments are about 125 ft thick near the base of the Puu Ka Pele slope, and may be 400–500 ft thick at the seaward edge of the Mana Coastal Plain. They lie on a gently sloping bench, apparently cut by waves into the original dome surface during a lower stand of sea level (Fig. 12).

The region west of the Waimea River, consisting of the Mana Coastal Plain and the Puu Ka Pele slope, is practically a rainshadow desert. This region receives an average annual rainfall of 18 inches (Table 1), the lowest rainfall of any major drainage area on the island. The lee coast has few fringing reefs, and those that do occur are more poorly developed than the reefs on the exposed windward coast.

⁷ Ruth Todd, U. S. Geological Survey, suggests that both species may thrive in water down to at least 200 ft (personal communication).

Before man changed the drainage in this area, most of the water that drained off of the Puu Ka Pele slope or that was discharged by springs from the ground-water body beneath the slope was ponded by the coastal sand dunes, forming a fresh to brackish marsh. Now even though the marsh has been drained, it seems unlikely that significant amounts of sediment are being supplied to the shore by streams other than the Waimea River. The presence of large calcareous dunes and the dominant marine nature of the sediments of the Mana Coastal Plain indicate the importance of the transport of biogenous material from the sea to the land. Prograding of the shoreline of the Mana Coastal Plain, during the recent geologic past, is indicated by the occurrence of multiple beach ridges west of Oomano Point, and at Mana by the lithified dunes situated two miles inland and parallel to the present coastal dunes at Nohili Point.

The carbonate content of the samples was high everywhere except near the Waimea River, where the sediments were principally terrigenous. The carbonate content increased towards the center of the Mana Coastal Plain, attaining a maximum value of about 90% at sample stations 8 and 9 (Fig. 11, top). The median diameter of the samples ranged from about 250 to 800 microns, with those near Nohili and Oomano Point being significantly coarser, probably as a result of increased wave action on the points.

There was a pronounced bimodality in the size distribution, both by sieving and settling tube, of sediments from stations 9 and 10. This seems to reflect the mixing of sediments from the Napali-Nohili region with those from the south coast. The major mode occurs at 180 microns, with a minor near 700 microns (Fig. 5). Microscopic examination shows the major mode to consist of unidentifiable fine, angular, carbonate grains; the principal constituent of the coarse mode was foraminifera, mostly *Heterostegina suborbicularis*. In comparison, sample 15, which consists of approximately equal portions of terrigenous and biogenous material, is better sorted and shows less tendency towards bimodality. Sample 15, which was collected nearly 3 miles west of Waimea River, is from a region of active littoral transport, where the rate of sorting approaches the rate of mixing of unlike materials. Carbonate content and size distribution of the sediments indicate that the terrigenous material is transported along the beach westward from the mouth of the Waimea River and southward from the Napali Coast, and that as it is transported it becomes progressively more diluted by biogenous material. The logarithm of the carbonate content is observed to increase linearly with distance from the Waimea River and from the Napali Coast (Fig. 11, bottom).

The increase in carbonate content with distance from the terrigenous source is indicative

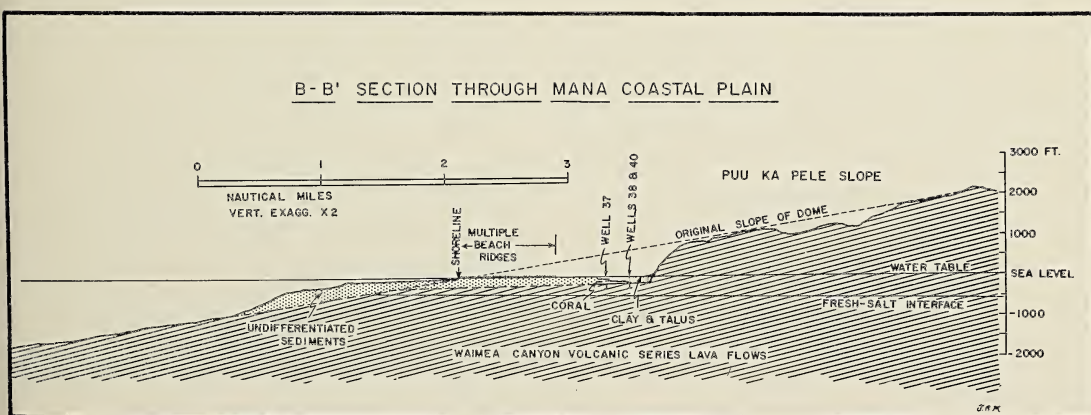


FIG. 12. Section through Mana Coastal Plain (along line shown in Fig. 11). Well numbers and well data taken from Macdonald, Davis, and Cox (1960). Composition of the submarine portion of the profile is little known and is based principally on the supposition that the section above the line of original slope of the dome is undifferentiated sediments, probably deposited by littoral currents at a lower sea level.

of continuous dilution by the addition of biogenous material. An expression giving the dilution rate can be derived under the following assumptions: (1) sand transported along the shore consists of a mixture of biogenous and terrigenous material, where the fraction of each is B and $1-B$ respectively; (2) this sand is transported along the shore at a rate Q which is constant with distance x along the coast; (3) biogenous material is supplied to the beach, from offshore, at a constant rate F_1 per unit of coast length, where it is completely mixed with the sand transported along the shore; and (4) there is a net deposition of this mixed sediment at a rate F_0 per unit of coast length, such that $F_1 = F_0$.

Conditions 1 through 4 lead to the following general expression for the concentration of biogenous material in the beach sand as a function of the longshore transport rate Q , the rate of supply of biogenous material F_1 , and distance along the coast x :

$$\ln B = \frac{F_1}{Q}x + \text{constant of integration}$$

where $\ln B$ is the natural logarithm of the carbonate fraction (see Appendix I). This is a straight line with slope F_1/Q when B is plotted on a logarithmic and x on a linear scale (Fig. 11, bottom). If the terrigenous material is supplied to the coast in large quantities and at a single point, as at the mouth of the Waimea River, B will be almost zero near the river and will increase exponentially with distance from the river—as it is observed to do.

The relation derived here is useful in that it not only predicts the form of the concentration change, but also indicates that, if either the longshore transport of sediment Q , or the deposition rate F is known, the other can be computed. The equation for the curve of concentration change with distance from the Waimea River is:

$$\ln B = 1.4x - 4.6$$

where $\ln B$ is the natural logarithm of the carbonate fraction, x is in nautical miles, and $F_1/Q = 1.4$ has the units of nautical miles⁻¹.

Neither F_1 nor Q are known, but very rough order-of-magnitude estimations can be made for both. The rate of accumulation of calcareous sediment on the Mana Coastal Plain, divided by the length of coast line, gives a measure of F_1 , while

the sediment yield from the Waimea River drainage basin provides an estimate for the littoral transport rate Q near the mouth of the Waimea River.

The volume of sediment in the Mana Coastal Plain down to a depth of 60 ft below sea level is approximately 4×10^{10} ft³. If it is assumed that 60% of this is of biogenous origin, and that it has accumulated along a coastal length of 15 nautical miles during a time interval of 8,500 years⁸, then the rate of supply of biogenous material to the coast, F_1 , is about 7000 cubic yd per mile per year. This gives a value for the littoral transport rate in the Waimea region of:

$$Q = F_1/1.4 = 5,000 \text{ yd}^3 \text{ per year.}$$

The Waimea drainage basin, with an average effective precipitation of 53 inches per year (Table 1), would be expected to yield about 420 tons of sediment per square statute mile per year (Langbein and Schumm, 1958: fig. 3). Assuming half of this to be sand-size or larger material, and using the conversion from weight to volume of 60 lbs per ft³ (given by Langbein and Schumm, 1958), one obtains a total yield of sand-size material from the Waimea basin of 25,000 yd³ per year. Since the Waimea River does not have a prograding delta, the yield from the river must nearly equal the littoral transport rate Q .

Beach surveys of 1926 and 1950 by the Corps of Engineers (1955: par. 52) indicated a net loss of sand from Waimea Beach of 5,000 yd³ per year. The littoral transport rate is probably greater than the loss, and the Corps of Engineers estimate it to be about 20,000 yd³ per year. Considering the nature of the assumptions leading to the calculations of littoral transport rate in the preceding paragraphs, values of 5,000 and 25,000 yd³ per year are remarkably, if not fortuitously, similar. One must recognize that, in so far as the actual transport rates at Waimea are concerned, these calculations may eventually prove to be merely a mental exercise. If this be the case, it is hoped that they have at least served to illustrate a valid principle.

⁸ The rate of 60 ft sea level rise in 8,500 years was selected because this seems to be the most accurate and significant part on the sea level rise curves, presented by Shepard (1960: fig. 4), McFarlen (1961: fig. 9), and Jalgersma and Pannekoek (1960: fig. 3).

ACKNOWLEDGMENTS

This paper represents, in part, results of research carried out by the University of California under contract with the Office of Naval Research. The original field work was performed in November and December 1955. Supplementary field study in January 1959 was supported by the Lihue Plantation Company, Kauai. Valuable advice and field assistance during the supplementary study was given by J. T. Orrick and S. L. Keala, Jr., of the Lihue Plantation. Since this study, North Kapaa Reef has been modified by dredging. Unfortunately the dredging was not performed entirely in accordance with plans based on the study of the littoral processes over the reef as outlined here. A north-south channel was dredged, which may intercept the sand supply to the beaches and cause the beach to erode.⁹

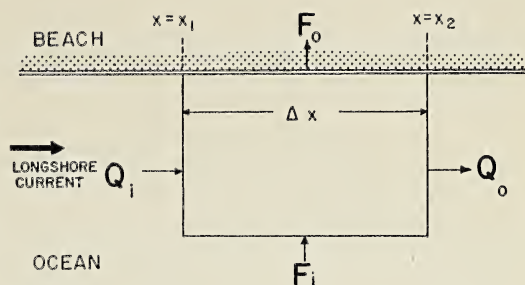
Valuable suggestions and guidance during the course of the study were contributed by R. S. Arthur, E. D. Goldberg, F. P. Shepard, E. W. Fager, and M. N. Bramlette of the University of California. Suggestions leading to the section on exposure to waves and wind were made by P. L. Horrer of Marine Advisers, La Jolla. Identification of foraminifera was made by Ruth Todd of the U. S. Geological Survey, Washington. In addition, the writers wish to express their appreciation to H. S. Ladd and J. I. Tracey, Jr., also of the U. S. Geological Survey, for their careful reading of the manuscript, and to Edith Haselwood of the Hawaiian Sugar Planters' Association for her editorial criticism.

APPENDIX I

DERIVATION OF SEDIMENT TRANSPORT EQUATION

A small segment of shoreline (see figure) is assumed to be in a state of equilibrium, such that the rate of longshore transport of material into the segment (the longshore influx) is constant and equal to the outflux, $Q_1 = Q_0$. Also, the onshore influx and outflux are constant and equal, $F_1 = F_0$. The sediment influx from offshore, F_1 , consists of 100% biogenous material,

⁹ Comparison of surveys of 1959 and 1962 indicate a net erosion of beach immediately westward of the dredging area (approximately stations 51–57, Fig. 8) of about 2,500 cubic yd per year.



Bi; while the sediment Q_1 transported longshore consists of two components, a terrigenous fraction T , and a biogenous fraction $B = 1 - T$. If complete mixing takes place within a coastal segment, having boundaries x_1 and x_2 , a distance Δx apart, then T is a function of the longshore distance x and can be written $T(x)$. The above assumptions permit the budget for the fraction of terrigenous material to be written:

$$Q \cdot T(x_1) = Q \cdot T(x_2) + F_0 T(x_1 + \frac{\Delta x}{2}) \Delta x$$

$$0 = \frac{Q T(x_1) - T(x_2)}{\Delta x} + F_0 T(x_1 + \frac{\Delta x}{2})$$

but in the limit as $\Delta x \longrightarrow 0$

$$0 = Q \frac{dT}{dx} + F_0 T(x)$$

$$\frac{dT}{T} = -\frac{F_0}{Q} dx$$

and integration gives $\ln T = -\frac{F_0}{Q} x + k$

where $\ln$ is the base of natural logarithms and k is a constant of integration. The relation may be written in terms of $B = 1 - T$ as:

$$\ln B = \frac{F}{Q} x + k$$

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NOTE

Adoption of the Metric System and Celsius Scale

The Intergovernmental Oceanographic Commission,

Noting that international adoption of the Metric System and Celsius Scale should be one of the major keys of promoting marine sciences,

Considering that the use of the Metric System was recommended by the Working Group on Data Exchange held in Washington from 7 to 10 August, 1962, (Ref: NS/IOC/2-5(c));

Noting further that data are to be submitted

to the World Data Centres in the Metric System and Celsius Scale.

Bearing in mind that for purposes of international exchanges of meteorological data, the World Meteorological Organization (WMO) has already adopted the said system at its 3rd Congress,

Recommends that member countries of IOC take the necessary steps to encourage, as far as possible, the use of the Metric System and Celsius Scale in their oceanographic publications.

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BATZO, RODERICK L., and J. K. RIPKIN. 1849. A Treatise on Pacific Gastropods. Rice and Shipley, Boston. vii + 326 pp., 8 figs., 1 map.

CRAWFORD, DAVID L. 1920a. New or interesting Psyllidae of the Pacific Coast (Homop.). Proc. Hawaii. Ent. Soc. 4(1): 12-14.

——— 1920b. The sandalwoods of Hawaii. Proc. Hawaii. Ent. Soc. 4(2): 374-375, 13 pls.

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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

TADAO YOSHIDA, TAKEO SAWADA, and
MASAHIRO HIGAKI
Sargassum at Tsuyazaki, North Kyushu

ALBERT TESTER
Role of Olfaction in Shark Predation

EDMUND S. HOBSON
Feeding Behavior in Three Species of Sharks

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Life History of Lepeophtheirus dissimulatus

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Effects of Pollution on Mytilus edulis

C. E. PEMBERTON
Insect Pests of Sugar Cane

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Sargassum Vegetation Growing in the Sea around Tsuyazaki, North Kyushu, Japan¹

TADAO YOSHIDA,² TAKEO SAWADA, and MASAHIRO HIGAKI³

ECOLOGICAL STUDIES on the subtidal marine vegetation, including the *Sargassum* community, have not progressed far because it is harder to make field surveys in subtidal vegetation than in terrestrial or intertidal vegetations. Some depth records for species of marine algae have been obtained using dredges and other instruments. From these data, we know that there is considerable vegetation developed at subtidal depths (cf Uéda and Okada, 1938, 1940).

Walker (1947) carried out extensive studies of the *Laminaria* beds around Scotland. His attention has been centered chiefly on productivity. Underwater observation of seaweeds has been done from time to time in the course of the development of diving apparatus. Waern (1952) published the results of his underwater survey of seaweeds. More recently Gilmartin (1960) carried out a survey of the deeper water algae of Eniwetok Atoll with the aid of a self-contained underwater breathing apparatus (SCUBA). Above all, a work published by Gislén (1930) is the most remarkable. He proposed a system of classification of life-forms for benthic plants and animals, and described many "associations." When these works are examined from a phytosociological point of view it is noticed that they are prescribed by the state of progress in terrestrial plant ecology at the particular time of writing. For example, Gislén only recognized associations in the concept of Swedish school and based on data from but a few quadrats.

Artificial stone beds have been laid down on shallow bottoms at many places around Japan for the propagation of useful algae, such as

Gelidium and *Undaria*. In order to evaluate the usefulness of these artificial stone beds many surveys have been carried out on the communities of algae developed upon them. However, the data secured from them are too rough to provide satisfactory knowledge of the marine vegetation and succession in its populations (Katada, 1958).

Many concepts and methods for the analysis of vegetational structure have been proposed recently in the course of the development of phytosociology. In contrast to the method of classifying the plant communities used by Braun-Blanquet and others, Goodall (1953) introduced a new statistical method for classification using positive interspecific correlation between the species as a criterion. On the other hand, Whittaker (1956) and others developed the concept of a vegetational continuum. These are applicable to the study of marine algal vegetations.

A *Sargassum* vegetation covers large areas of the upper subtidal region of the warmer waters around Japan. This vegetation affords a good habitat or spawning bed to many kinds of fish. Plants of *Sargassum* and its allied genera, floating at the sea surface after being detached from their substrata, are known as "floating seaweeds" or "nagaremo." The floating seaweeds and many kinds of fish exist in a close relationship insofar as the fish spawning and growth of the larvae of the fish are concerned. The authors have been engaged in the survey of the floating seaweeds for several years, and feel acutely the necessity for knowledge concerning the *Sargassum* community from which the floating seaweeds of Japan are derived. The authors carried out a survey on the *Sargassum* community growing on the rocky shallow sea around Tsuyazaki, north Kyushu, Japan, and intend to analyse here the relationship of species populations to the gradient of environmental factors.

¹ Contribution from the Department of Fisheries, Faculty of Agriculture, Kyushu University. Manuscript received November 23, 1961.

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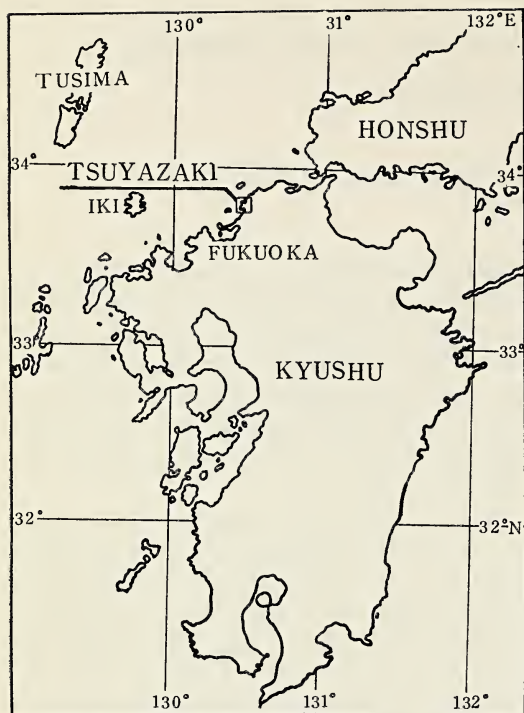


FIG. 1. Map of Kyushu, showing the position of Tsuyazaki.

DESCRIPTION OF AREA SURVEYED

The peninsula of Tsuyazaki (Fig. 1) lies at $130^{\circ} 29' E$, $33^{\circ} 47' N$, about 20 km north-northeast of Fukuoka City, and faces on the Genkai-nada. The peninsula protrudes from general coast line of sandy beach, and consists of hills more than 100 m high. Although these hills are for the most part composed of palaeozoic sedimentary rock, there is a granite zone on the west side facing the sea, and a basalt layer lying above the 100 m contour line. Along the middle of the shore of the peninsula, there is a sandy beach called "koi-no-ura." The rocky area, where the *Sargassum* community develops, occupies the northern and southern parts of the peninsula. An outline of the geological structure of the area concerned is shown in Figure 2.

Although the nature of the bottom is rocky where the shore is exposed to strong wave action from the intertidal zone to a depth of about 10 m, or of boulders in more sheltered places, such hard bottoms give way to sand at the relatively shallow depth of 15 m or less. Sandy

bottoms are met in deeper places all around the peninsula.

On the coast of North Kyushu, tides are semi-diurnal, and the diurnal inequality of the tides is not remarkable. The spring tidal range is about 1.9 m, and 1.4 m at neap tide. According to the "Coast of Kyushu Pilot" (1947), in the Kuraraseto passage, lying to the north-northeast about 10 km from Tsuyazaki, the tidal current flows towards the north from 4 hr after low tide to 4 hr after high tide, and towards the south from 4 hr after high tide to 4 hr after low tide. The tidal current flowing north reaches a speed of 2.8 knots. Near the shore of the area surveyed, the tidal current runs even faster around Tsuzumi islet, lying to the north of the peninsula, and may reach a maximum speed of more than 1 knot. The current moves more slowly near Sone-no-hana and Kyôdomari.

Stronger waves and swells are generated with north or west winds, influenced by the topography of the neighbouring area. Hence, the north and west sides of the peninsula are more ex-

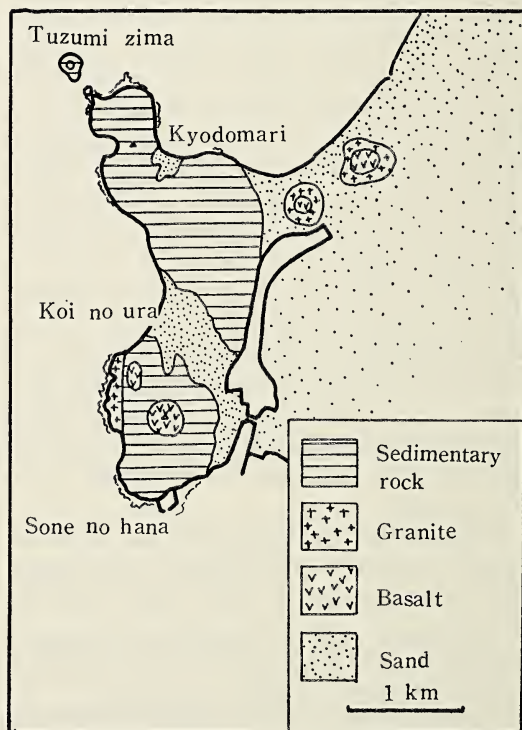


FIG. 2. Geological map of the peninsula of Tsuyazaki (after Takehara, 1937).

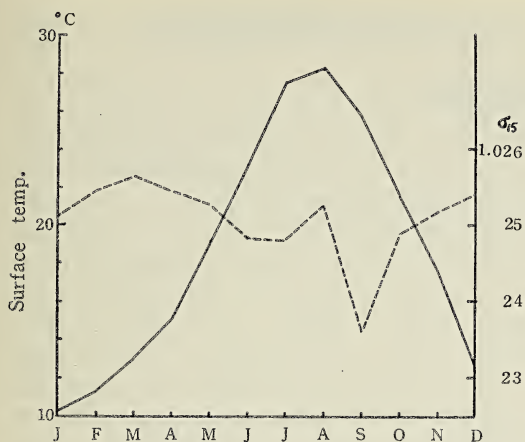


FIG. 3. Seasonal variation of surface temperature (solid line) and specific gravity (dotted line) of the sea water for 1960, measured at the top of the break-water for the port of Tsuyazaki.

posed to wave action. The eastern sides of Sone-no-hana and Kyôdomari are more sheltered from wave action, although there is no method of determining the strength of wave action, judging from the results of direct observation of waves and from the characteristics of the intertidal algal zonation.

The tidal current is faster where the shore is more exposed to wave action, and vice versa in the area surveyed.

Surface temperatures rise to about 28 C in August and descend to about 10 C in January (Fig. 3). Transparency of the sea water is less than 15 m in the Secchi disc reading almost throughout the year. After a heavy rain, low transparency is sometimes recorded around Sone-no-hana.

METHODS

Field surveys were carried out during 7 days between July 23 and August 26, 1959, on 13 survey lines in the area (Fig. 4), as follows. A survey ship was anchored at the offshore end of each line. A rope was then strung from the ship to a rock on the shore. Survey spots were selected along the rope every 5 or 10 m depending on the inclination of the bottom. One or two observers, a recorder, and a crew got into a small boat. The boat halted at each survey spot. The depth of water was measured with a sound-

ing lead and then a quadrat was laid down. The quadrat used in this study was a 0.5 m square iron frame. Observations on the plants found in the quadrat were made by skin diving, using a face mask only. First, the percentage of vegetational cover of the area around the quadrat was recorded. Then, the degree of cover by each species of the algae present in the quadrat was measured. The scale for the measurement of cover degree was as follows:

+	0- 10%
1	11- 20%
2	21- 40%
3	41- 60%
4	61- 80%
5	81-100%

Number and height of the plants were recorded when this was possible. The species not present in the quadrat but found in the surrounding area were also noted.

The number of quadrats placed along each

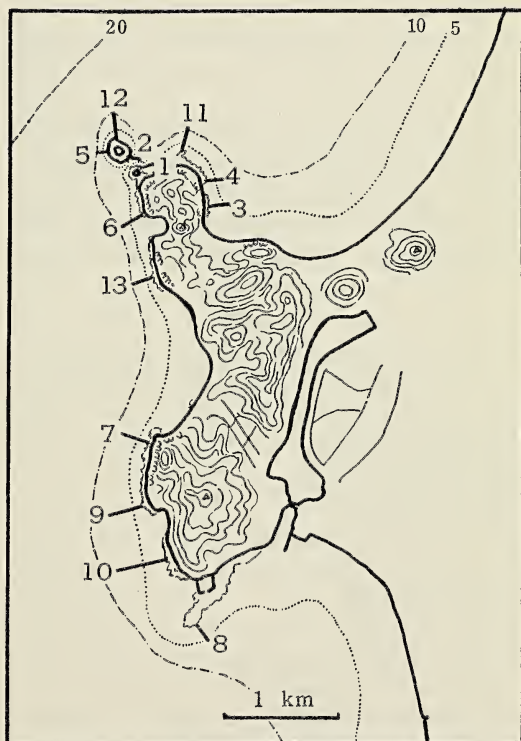


FIG. 4. Map of Tsuyazaki peninsula, indicating the 13 survey lines.

survey line varied from 10 to 20, according to the inclination of the bottom; 197 sets of quadrat data were obtained. All data needed for analysis were recorded on hand-sort edge-punched cards to facilitate the compilation of the data. Readings of depth were adjusted to the low watermark of spring tide, and the quadrat of 0 m level indicates the quadrats placed above the low watermark. The depth represented as 1 m concerns the quadrat level laid down between low watermark and 1 m deep, and so on.

RESULTS

Stratal Structure of Sargassum Community

Twelve species of *Sargassum*, one species of *Cystophyllum*, and one species of *Hizikia* occurred in the quadrats surveyed (Table 1). The fruiting period of these species is revealed by analysing the data obtained from surveys of the floating seaweeds (Segawa, Sawada, Higaki, and Yoshida, 1959). According to these results and our observations made at the stations investigated, all of the species growing there except *Sargassum ringgoldianum* had passed their fruiting period. Most of the individuals of each perennial species had lost their long branches bearing the receptacles, and most of the branches of the next year class had reached a length of 30–40 cm. Therefore, the vegetation was at its lowest height for the year. However, *S. ringgoldianum* was taller than the rest. Annual

species such as *S. horneri* were in a very early stage of growth. At the time of the year when the survey was done, therefore, all species of *Sargassum* were considered to contribute to the same layer, and cover degree of the species was rather easy to determine. Stratal difference may be developed among the species of *Sargassum* during the period from winter to spring, because of the difference in the growing and fruiting periods of the species concerned (cf Segawa, Sawada, Higaki, and Yoshida, 1960). Species other than *Sargassum* occurred mainly at shallower places, and there was almost the total lack of a frondose lower layer under the well-developed layer of *Sargassum*. The crustose layer was represented by species of unarticulated corallines. In the area where the upper layer was open because of the absence of *Sargassum*, several species of frondose algae other than *Sargassum* formed a lower layer. Although the population of *Sargassum* became sparse in deeper places, the society of the lower frondose strata was not developed. This fact may be attributed partly to the survey time, when many kinds of algae were extremely depauperate in growth for the year.

Vertical Distribution of Species

The substratum profile and the vertical distribution of some of the major species of *Sargassum* are presented (Fig. 5) for each station.

At station 1 (Fig. 5), the rocky bottom is evenly sloped to a depth of more than 8 m, then it gives way to sand. The dominant species of *Sargassum* changes with increasing depth: *S. piluliferum* is predominant at depths less than 3 m, then *S. patens* predominates over the other species on rock surfaces about 3 m deep, and finally *S. serratifolium* predominates in deeper places. On the other hand, at station 6 (Fig. 5), the bottom is of boulders for the most part and there is some solid rock bottom in places. The slope of the bottom is lower than at station 1. While three of the species of *Sargassum* just mentioned are also present here, their degree of cover and vertical range do not coincide with what was found at station 1. As stated above, the vertical ranges of the species are not the same among the stations surveyed. An explanation for these differences is desirable.

TABLE 1
SPECIES OF *Sargassum* AND RELATED GENERA
OBSERVED IN QUADRATS

<i>S. thunbergii</i> (Mertens) O. Kuntze
<i>S. nigrifolium</i> Yendo
<i>S. hemiphyllum</i> C. Agardh
<i>S. confusum</i> Agardh
<i>S. micracanthum</i> (Kützinger) Yendo
<i>S. ringgoldianum</i> Harvey
<i>S. fulvellum</i> Agardh
<i>S. patens</i> C. Agardh
<i>S. tortile</i> C. Agardh
<i>S. yendoii</i> Okamura et Yamada ?
<i>S. piluliferum</i> C. Agardh
<i>S. serratifolium</i> J. Agardh
<i>Cystophyllum sisymbrioides</i> J. Agardh
(= <i>Myagropsis myagroides</i> (Turner) Fensholt)
<i>Hizikia fusiforme</i> (Harvey) Okamura

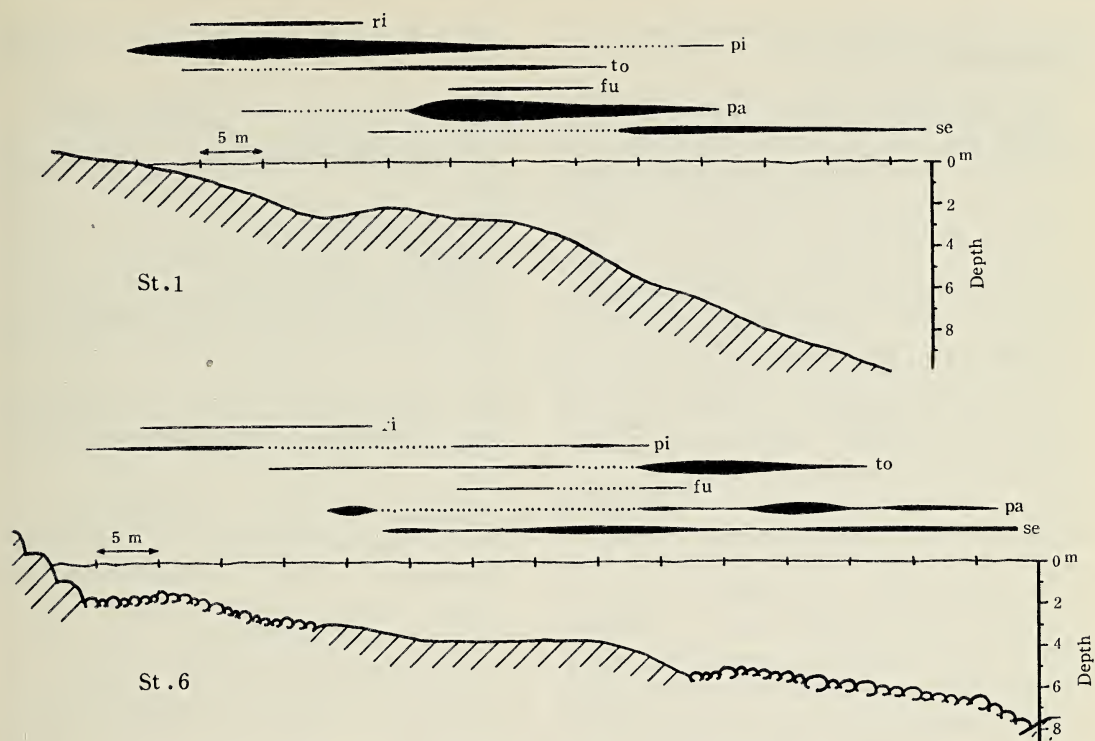


FIG. 5. Profile of substratum and distribution of species: ri, *S. ringgoldianum*; pi, *S. piluliferum*; to, *S. tortile*; fu, *S. fulvellum*; pa, *S. patens*; se, *S. serratifolium*.

Vegetational Cover

The percentage of vegetational cover was approximated by eye for several square meters around the spot where the frame of the quadrat was laid down. For this measurement, crustose algae were not included. As shown in a later section, algae other than *Sargassum* were found mostly in the relatively shallow places and had only a slight effect on the degree of vegetational cover in the deeper places.

Variation in average vegetational cover with increasing depth was determined using the whole quadrat samples. This mean value is indicated with a dotted line in Figure 6. From this figure it can be seen that the average vegetational cover is nearly uniform from the low watermark to 5 m deep, and then decreases gradually in places beyond the 5 m depth. Here only depth of water is taken into consideration as an environmental factor.

In this study, the 13 stations surveyed are placed in three groups according to the strength of wave action. For each of the three groups,

then, the relationship between the depth of water and average vegetational cover is plotted in Figure 6 by the three solid lines. At the rather sheltered stations subject to weak wave action, the maximum value for average vegetational cover is found at the 1 m depth. As deeper water is reached the values fall quickly. For the areas where wave action is moderate, vegetational cover reaches its maximum 2–3 m below low watermark and gradually decreases with increasing depth. An examination of the values from the stations exposed to the strongest wave action shows the values for average vegetational cover reach 100% above the low watermark, then fall and again come to a peak at the depth of 4–6 m. Algae other than *Sargassum* contribute to the vegetational cover in shallower places exposed to strong wave action. Therefore, when the degree of cover for *Sargassum* only is considered, the depth at which the maximum value for vegetational cover is found becomes deeper with increasing strength of wave action.

Distribution of Species Populations along Environmental Gradient

The distribution pattern of the populations of *Sargassum* may not be understood when only the depth of water is taken into consideration as an environmental factor. The effect of the wave action on it must be considered at the same time. The survey stations are classed in three groups according to the degree of wave action, as shown above. Average degree of cover of each species is plotted against depth. For five major species, the curves of average degree of cover were superimposed to obtain the graph represented by Figure 7. The curve for each individual species overlaps the others and the peaks of the different curves occur at different depths. For the places moderately exposed to wave action (Fig. 7, lower graph), the curve for *S. hemiphyllum* has its peak at a depth of 1 m below low watermark, that of *S. ringgoldianum* comes second, and next in order are *S. piluliferum*, *S. patens*, and *S. serratifolium*, from the shallowest to the deepest. In places subjected to stronger wave action (Fig. 7, upper graph), the order of appearance is the same as above, but the peaks of the curves for degree of cover occur deeper, except in the case of *S. ringgoldianum*.

The method of gradient analysis developed

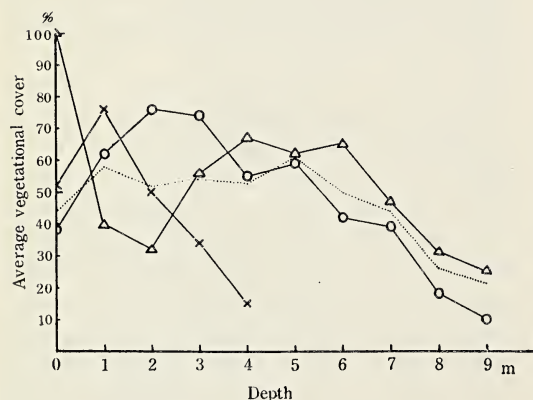


FIG. 6. Variation of average vegetational cover in relation to depth of water.

- Average of whole quadrat data
- x — x Sheltered
- o — o Moderate wave action
- Δ — Δ Exposed

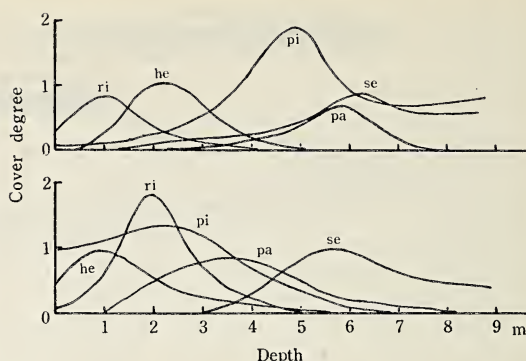


FIG. 7. Change of cover degree in relation to depth of water. (Abbreviation of species names as in Fig. 5.)

by Whittaker (1956) is introduced here to make the distribution pattern of these *Sargassum* species more clear. The depth of water and exposure to wave action are considered as the principal environmental gradients. The population nomograms for six major species constructed on this basis are shown in Figure 8. *S. serratifolium*, *S. piluliferum*, and *S. hemiphyllum* have their peaks at the stations exposed to stronger wave action, but their peaks occurred at different depths, in the order given, with *S. hemiphyllum* at the shallower end of the series. The species which occurred more abundantly at the places subject to more moderate wave action are *S. ringgoldianum* and *S. fulvellum*. The former grows more abundantly at places of 2 m depths where the bottom is hard and wave action is moderate. It has a tendency to grow in shallower places with both increasing and decreasing strength of wave action. This bimodal distribution pattern is peculiar to this species only. Only young individuals of *S. fulvellum*, an annual species, were found when the investigation was carried out, and the degree of cover of this species was very low. Nevertheless a population nomogram of distinctive pattern was obtained. *S. patens* and *S. tortile* grow abundantly on bottoms more sheltered from wave action. However, the population nomogram for one species differs more or less from the others in the position of maximum value, even if the distribution patterns are similar to each other. Generally speaking, most species of *Sargassum* grow in deeper places as the strength of the wave action increases.

Objective Classification of Sargassum Community

Goodall (1953) proposed a method of dividing vegetation samples into statistically homogeneous groups. This method involves preparing a 2 × 2 table whereon the correlation between every pair of species is analysed by computing a value from the number of quadrats in which one or both of two particular species are present or not. An objective classification can be arrived at when, with respect to all species growing in the sample quadrats, no interspecific correlations of significant level occur within each group of quadrats, so that the quadrats may be divided into some homogeneous groups. The significance of interspecific correlation is decided by χ^2 test, preparing the 2 × 2 table, as shown below:

		SPECIES B		
		present	absent	
Species A	present	a	c	a + c
	absent	b	d	b + d
		a + b	c + d	n = a + b + c + d

$$\chi^2 = \frac{(ad-bc \pm n/2)^2 n}{(a+b)(c+d)(a+c)(b+d)}$$

Values of χ^2 are calculated between every pair of the six species of *Sargassum* contained frequently in quadrats, and are shown in Table 2. Only two combinations, i.e., the pairs of *S. ringgoldianum*–*S. piluliferum* and *S. tortile*–*S. patens*, have significant correlation at the 5% level. According to the first procedure of classification proposed by Goodall (1953: 46–50), as a result of the elimination of quadrats containing one species of high frequency in those four species mentioned above, no species was

found which has a significant interspecific correlation with the others in the final two groups obtained. However, the two groups obtained from this procedure are not useful because quadrats belonging to one group are considerably intermixed with the others.

Distribution of Algae Other than Sargassum

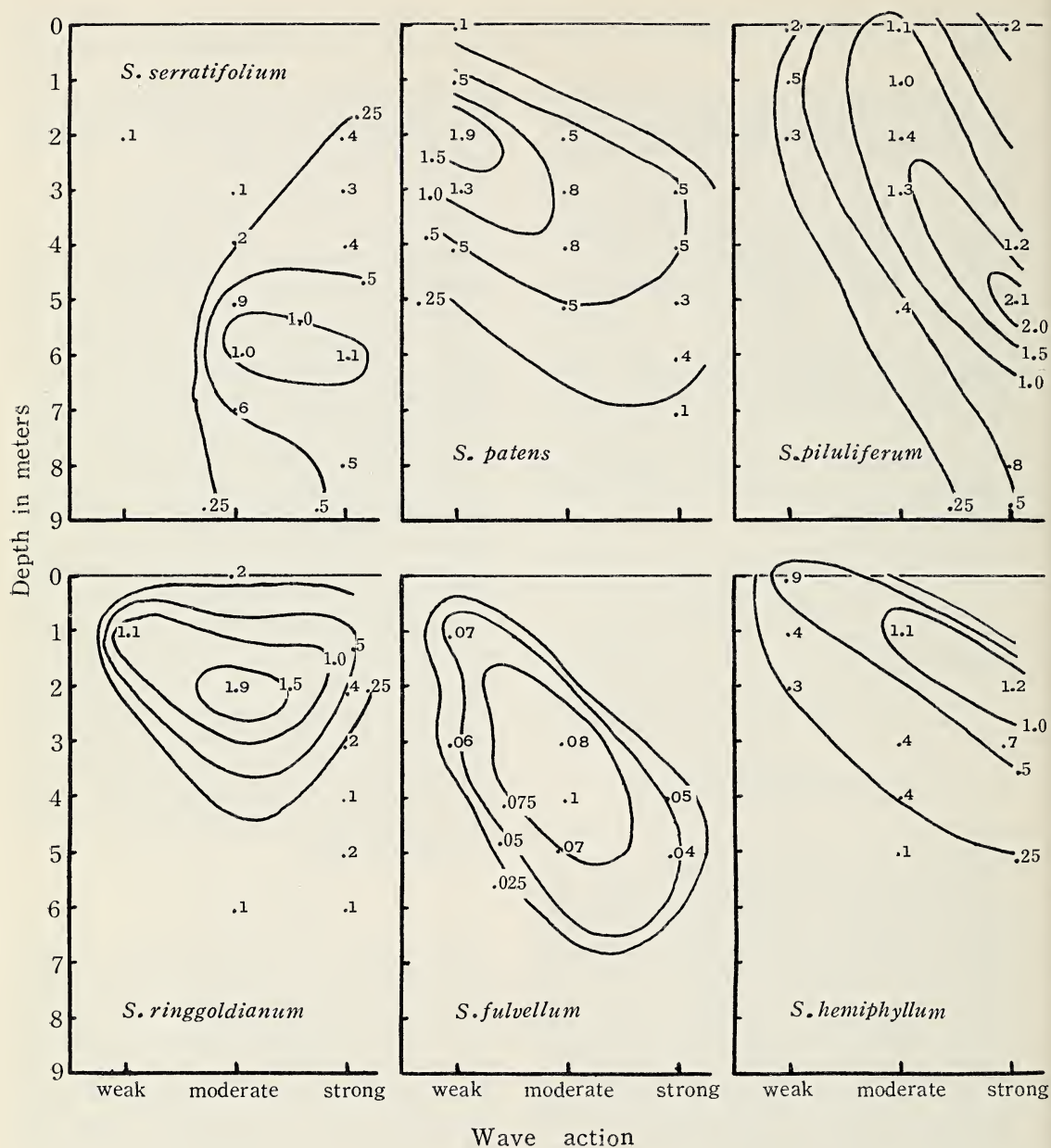
Although attention was not centered on the distribution of algae other than *Sargassum*, observational data on those algae were recorded as often as possible. The species observed in this survey are listed in Figure 9. The frequency of quadrats containing algae other than *Sargassum* is calculated for each depth, and the graph in Figure 10 is the result. This graph illustrates that the species other than *Sargassum* occurred in all quadrats laid above the low watermark, but that the frequency of their occurrence in quadrats decreases sharply with increasing depth. The range of the species growing at different depths is shown in Figure 9. *Dictyopteris undulata* was observed in the deepest quadrat. The marine vegetation was richest in number of species at the place exposed to the strongest wave action, and more abundant in number of individuals near the low watermark. At deeper places the density of algae is less and the vegetational cover may be provided by the species of *Sargassum* alone.

DISCUSSION

With respect to the stratal structure of the marine algal community, Segawa considered that three layers are recognized, i.e., the upper, lower, and crustose layers, when a well-developed vegetation is being considered (Katada, 1958). The upper layer is more than 10 cm in height, and the crustose layer is composed of algae less than 1 cm high. At the time of the year when

TABLE 2
 χ^2 —VALUES BETWEEN SIX SPECIES OF *Sargassum* FREQUENTLY ENCOUNTERED

	<i>S. hemiphyllum</i>	<i>S. piluliferum</i>	<i>S. ringgoldianum</i>	<i>S. tortile</i>	<i>S. patens</i>
<i>S. serratifolium</i>	6.093	2.652	4.330	2.923	1.661
<i>S. patens</i>	0.517	7.337	6.391	8.405	
<i>S. tortile</i>	2.527	0.045	0.000		
<i>S. ringgoldianum</i>	2.197	9.776			
<i>S. piluliferum</i>	3.772				

FIG. 8. Population nomograms for six major species of *Sargassum*.

this survey was made, all the species of *Sargassum* found in the subtidal region formed but a single upper layer, and there was no constituent in this layer other than *Sargassum*. Katada reported that *Undaria pinnatifida* may also be included in this layer, intermingled with *Sargassum*.

As already pointed out, in reference to the population nomograms in Figure 8, the *Sargassum* community appears to form a continuum. This is confirmed by the application of Goodall's objective method of classification. Hence it is desirable that our attention be centered on the distribution of each species popu-

lation in relation to the gradient of environmental factors, rather than centering it on classifying the communities.

The junior author has reported that the vertical distribution of a species of *Sargassum* is hardly explained when only the depth of water is taken into consideration, and that, in addition, presence or absence of a species at a certain station may partly be determined by the degree of exposure to wave action (Yoshida, 1961). At present, our knowledge is insufficient to elucidate the detailed effect of many environmental factors on the distribution of the species. For marine plants, increasing the depth of water has an important effect on growth in connection with the diminishing intensity and variation in the spectrum of the light penetrating into the water. On the other hand, we must take into account the other environmental factors, such as wave action or the turbulence of water. There is also a resultant complex of several factors. According to Gessner (1955:198–209), the movement of water may have a close relationship with the assimilation and respiration rates of marine algae. It has already been re-

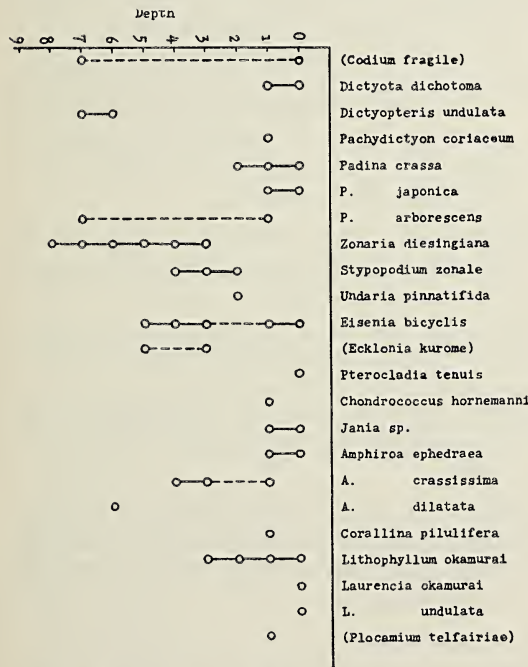


FIG. 9. Vertical ranges of distribution of algae other than *Sargassum*. Species in parenthesis did not occur in quadrats.

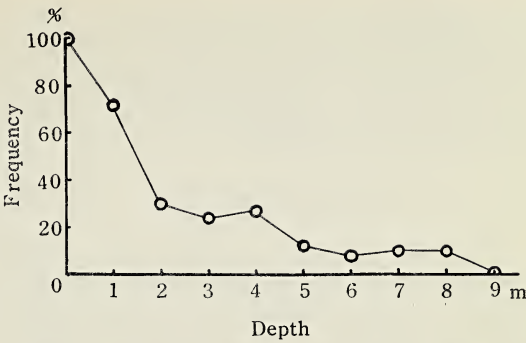


FIG. 10. Frequency in occurrence of algae other than *Sargassum* (cf Fig. 9) in relation to water depth.

ported that the distribution pattern of intertidal organisms is greatly affected by the turbulence of water (Southward and Orton, 1954). In this present study the distribution pattern of the species of *Sargassum* is clearly shown by the two-dimensional gradient analysis improved by Whittaker (1956). Two principal environmental gradients considered here are (a) the depth of water, and (b) the exposure to wave action. In the area surveyed the tidal current is faster where the shore is exposed to the stronger wave action, as stated above. It is hardly possible to treat the two factors, namely, exposure to wave action and speed of tidal current, independently.

Determining the lower limit of the marine vegetation was prevented by the diving ability of the observer. It is observed around Tsuzumi islet that the species of *Sargassum* grow at places deeper than 10 m, where hard bottoms are found. At most of the stations, the hard bottom gives way to sand before what would seem to be the lower potential limit for *Sargassum* growth is reached.

SUMMARY

The *Sargassum* community found in the upper part of the subtidal region in the sea around Tsuyazaki, North Kyushu, Japan was studied phytosociologically in July and August, 1959. It seems that this community can not be divided successfully into smaller groups by applying Goodall's objective method of using positive interspecific correlation. The gradient analysis method developed by Whittaker (1956)

was applied here to the major species of *Sargassum*. Two principal environmental gradients considered here are depth of water and exposure to wave action. The stratal structure of this community is also noted.

ACKNOWLEDGMENTS

The authors wish to express their sincere appreciation for the guidance of the late Professor S. Segawa throughout this study. Their heartiest gratitude is due Professor T. Hosokawa, of the Faculty of Science, Kyushu University, and to Professor Maxwell S. Doty, of the University of Hawaii, for their kind advice and criticism of the manuscript. The authors' thanks are also due Mr. T. Furukawa in the Fishery Research Laboratory, Kyushu University, who assisted them in the course of the field survey.

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The Role of Olfaction in Shark Predation¹

ALBERT L. TESTER²

IT IS RECOGNIZED that most if not all species of sharks possess a keen sense of smell which is used in detecting dead and wounded prey or other edible material during their well-known scavenging operations. The early experiments of Parker (1910), Sheldon (1911), and Parker and Sheldon (1913) established the role of the paired nasal organs as olfactory receptors. Parker (1914) demonstrated directional response in the smooth dogfish (*Mustelus canis*) and provided a plausible explanation of how this was accomplished; he postulated that the two separated nostrils have the ability to detect small differences in the concentration of odorous materials enabling the shark to orient in the direction of equal stimulation and to head "upstream" to the source. This tracking ability is well recognized by skin divers and fishermen who have involuntarily attracted sharks by retaining speared fish or by discarding trash fish and offal from their boats.

It seems unlikely that any shark species could maintain itself entirely by scavenging operations, except perhaps in areas where man provides forage such as bait, fish offal, or other forms of edible garbage. Certainly the larger species are recognized as active predators which attack uninjured living prey, including man. Doubtless, vision plays a predominating role in locating and tracking normal living prey, and possibly other senses such as hearing are also involved. In considering olfaction, attention has

focused largely on feeding activity induced by the release of attractive substances such as blood or other body fluids from the wounds of injured prey. The possible part played by olfaction in the detection and tracking of uninjured living prey has been largely overlooked.

In this paper I will present the results of experiments on the olfactory response of captive sharks to extracts of natural foods, to human materials, and to uninjured living fish in the hope of clarifying the role of olfaction in shark feeding activity. The results form part of an investigation of factors affecting the behavior of sharks sponsored by the Office of Naval Research (Contract Nonr 2756(00), Project NR 104503) over the period 1959-61. The work was undertaken at the Eniwetok Marine Biological Laboratory, Eniwetok Atoll, Marshall Islands, and at the Hawaii Marine Laboratory, Oahu, Hawaii. I am grateful to the respective directors, Dr. R. W. Hiatt and Dr. A. H. Banner, for laboratory facilities. I am indebted to personnel of the Atomic Energy Commission and the Pacific Missile Range Facility for logistic and other help. I am particularly indebted to those graduate students who have assisted in phases of the project: Edmond S. Hobson, Susumu Kato, Taylor A. Pryor, and Bori L. Olla.

FACILITIES, MATERIALS, AND METHODS

Eniwetok Marine Biological Station

At Eniwetok, small (18-36 inches) blacktip sharks (*Carcharhinus melanopterus*) and small (20-36 inches) grey sharks (*C. menisorrh*) were readily caught in shallow water by hook and line and established in captivity. Holding facilities consisted of two large concrete tanks housed in a building and illuminated by overhead fluorescent lighting (Fig. 1). The tanks were supplied with running sea water pumped

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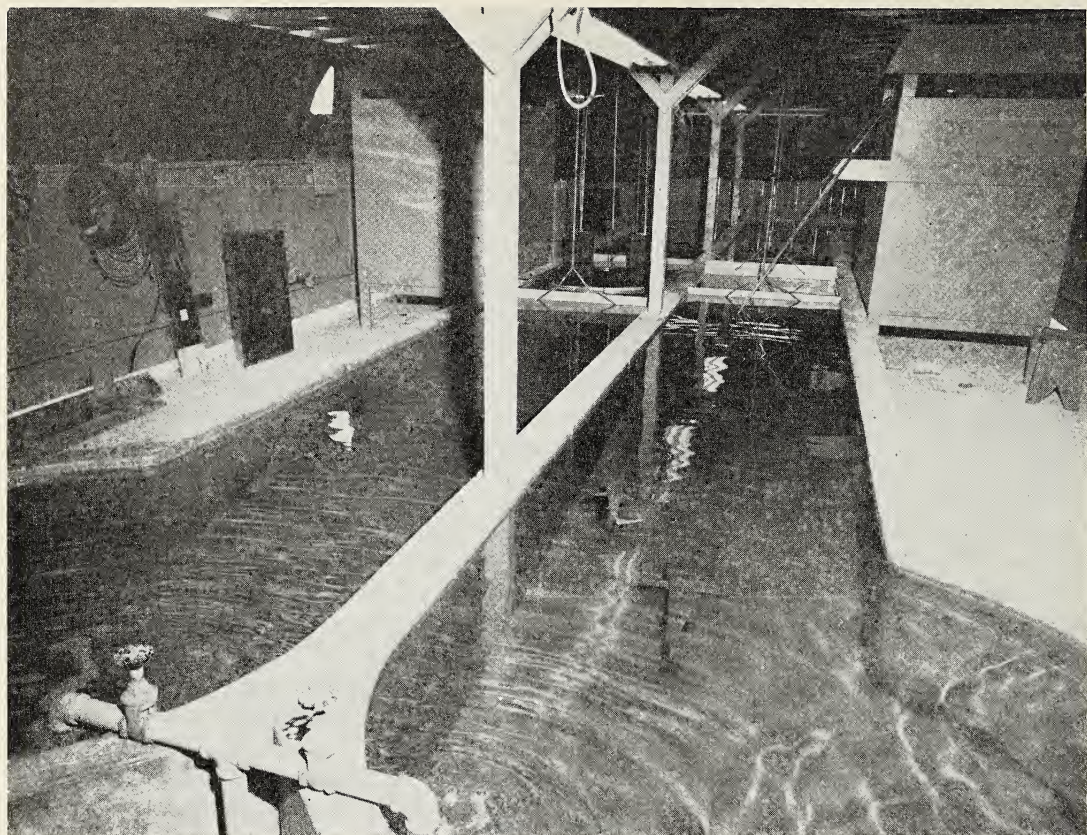


FIG. 1. View of shark tanks at Eniwetok Marine Biological Laboratory. (Photograph by Atomic Energy Commission.)

from the lagoon at a maximum rate of flow of about 10 gal per min. Lying side by side with a common middle wall, the tanks were 50 ft long, 4 ft wide and 3 ft deep with turning basins 6 ft in diameter at both ends (Fig. 2). The tanks could be divided into 5-ft sections by gates which slid in notches in the walls. Thus the sharks could be confined in a compartment consisting of one or several sections. Observation booths located midway along the tanks on both sides or blinds erected elsewhere effectively concealed the observer from the sharks.

Olfaction tests were conducted on both "normal" and blinded sharks. The sharks were blinded after anesthesia in a 1/1000 solution of MS 222- Sandoz (cf Gilbert and Wood, 1957) by coagulating the proteins of the aqueous humor with the diode probe of a "Hyfrecator" inserted through the cornea. Proof of blindness

was lack of response to a hand waved close to the surface as they swam by or lack of response to the beam of a flashlight directed at their eyes. Within 1 hr after recovery from anesthesia the sharks circled their compartment, guided by the tip of the outstretched pectoral fin which touched the wall. Within a day they were able to circle the compartment without this tactile aide. They soon fed avidly on pieces of fish, squid, or other food which settled to the bottom before it was eaten. The sharks would detect the odor while swimming in mid-water and would spiral down, converging on the food by swimming in a figure-8 pattern on the bottom. Our attempts at blinding sharks with contact occluders (Mishkin, Gunkel, and Rosvold, 1959) were unsuccessful, perhaps because of faulty technique in molding plastic "lenses" and fitting them to the eyes. In general, the response of

the blinded sharks to olfactory substances was considerably less variable than that of sharks with normal vision.

Except during starvation experiments, the sharks were fed sparingly about once or twice a week; uneaten food was removed to avoid putrefaction and an unnecessary increase in olfactory level.

After investigating several different techniques during the early summer of 1959, a standard method of testing materials which could be dissolved or suspended in water was adopted. With natural foods such as fish flesh, usually 5 gm of material was macerated in a Waring blender for 5 min with 250 ml of fresh water; sea water was not used because essential oils tended to accumulate in the froth. The material was then filtered and held in a refrigerator until used. Prior to an experiment a small quantity (usually 3.0 ml) of the clear solution was diluted with sea water to 25 ml in a test tube and then further diluted to 100 ml with sea water in a funnel. Substances other than natural foods were diluted to various concentrations before being tested.

Prior to testing, a glass funnel and tube leading from the observation booth to a point just below the surface in the center of a test area (e.g., Fig. 2, Tank 1, D) was filled with sea water to remove air bubbles; the contents were maintained by closing a pinchcock. The flow of sea water to the tanks was shut off at the inflow valve. Usually, five 2-min control periods were then run, during each of which the time (seconds) spent by one or more of the sharks in the test areas (e.g., Tank 1, C and D) was recorded by an electric timer activated by a foot switch. At the same time, observations were recorded of the behavior of the sharks and sometimes of the number of passes or turns in the test areas. The test material was then introduced silently while the sharks were at the far end of the compartment, and the activity of the sharks was again noted and recorded during five (or more) 2-min test periods. The nature of the response was then categorized as attraction, repulsion, etc. on the basis of the graphed data and the notes.

A similar technique was used in 1960 except that timing was abandoned in favor of counting the number of turns. Each of the two test areas

was divided by an imaginary line into halves; turns in the four half-areas were given weights of 1 to 4, with the weights increasing toward the half-area of introduction (Fig. 2). The graphed "count index" of activity seemed to reflect our subjective impression of a response

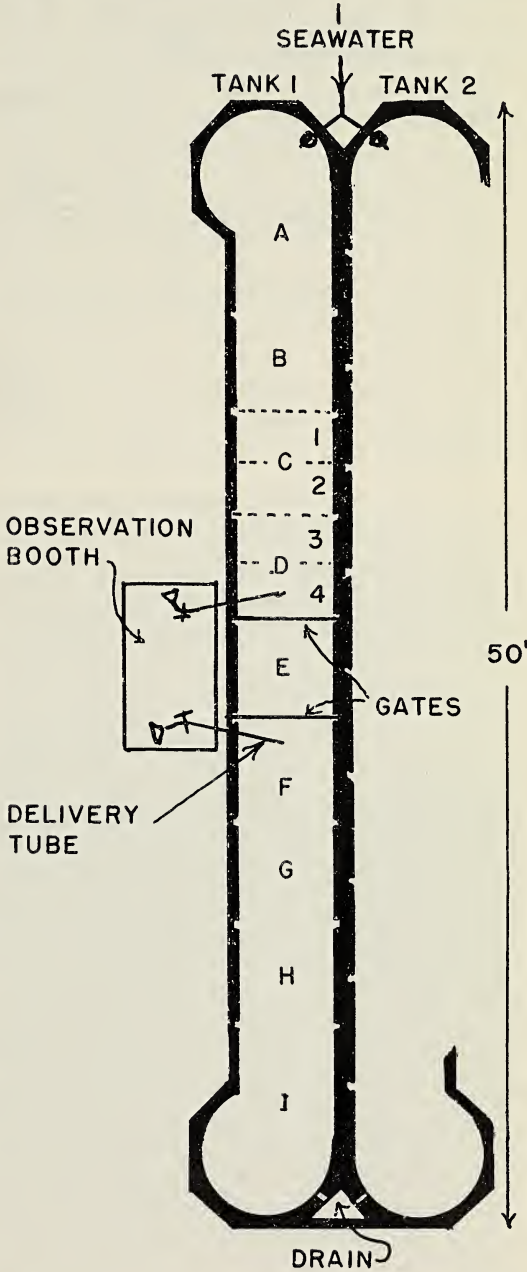


FIG. 2. Diagram of shark tanks at Eniwetok Marine Biological Laboratory.

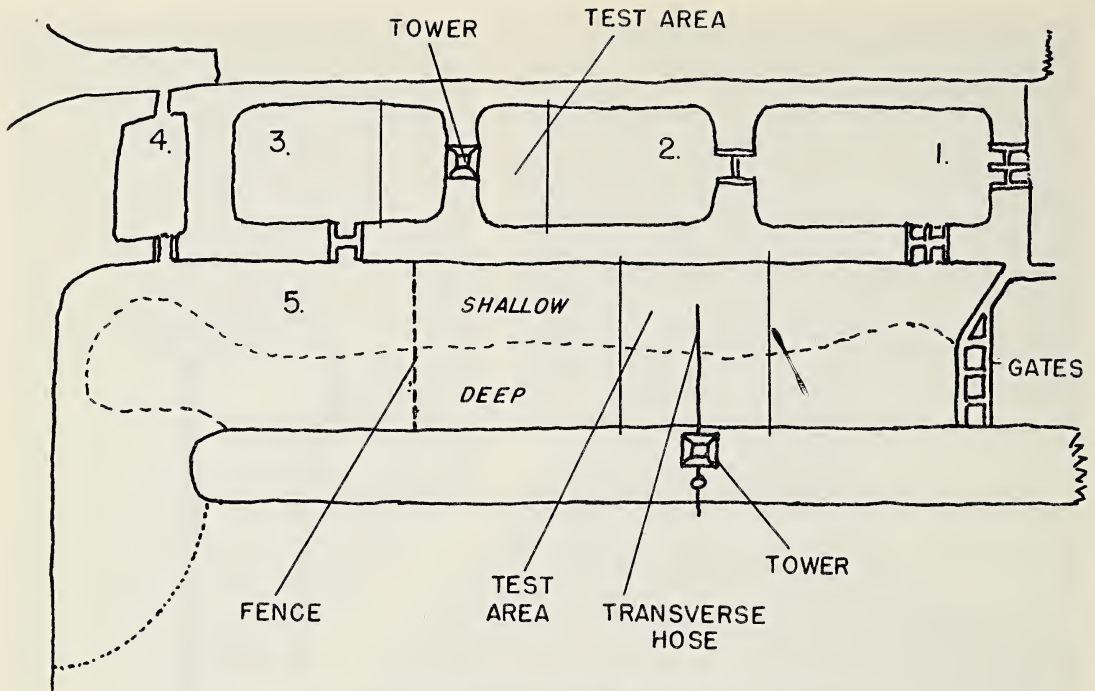


FIG. 3. Diagram of pond arrangement at Hawaii Marine Laboratory.

more realistically than the "time index." Special techniques used in studying the response of the sharks to living fish will be discussed later.

Hawaii Marine Laboratory

At the Hawaii laboratory several grey sharks of two species (*Carcharhinus* spp.), hammerhead sharks (*Sphyrna lewini*), and tiger sharks (*Galeocerdo cuvier*), all 5 to 7 ft in length, were readily caught by set line in the adjacent waters of Kaneohe Bay. They were established in large seminatural ponds (Fig. 3), screened by gates and flushed slowly by tidal action. Three grey sharks and one tiger shark were successfully maintained in captivity for 3 years and were still alive and healthy at the time of writing (October 1961). Hammerheads were successfully maintained in captivity for periods from 3 months to 1 year. It is suspected that their death was due either to injury caused by the other sharks or lack of food. They were unable to compete successfully with the fast, aggressive grey sharks; often our efforts at preferential hand-feeding failed when the food was taken persistently by the other species. The

sharks were fed sparingly about once or twice a week on cut or whole fish.

Several experiments were undertaken on a tiger shark and a grey shark following their respective establishment in Ponds 2 and 3, both of which were about 100 ft long, 60 ft wide and 3–4 ft in maximum depth. Observations were conducted from a 16-ft tower between the ponds. By means of a pump and hose a continuous flow of water was taken from one pond, led to the top of the tower, and thence led into a test area of the other pond. Following a series of 3-min control periods, during which quantitative data were collected on the activity of the shark, notes were made of overt responses and the path of the shark was diagrammed. The material to be tested was then introduced into the stream of salt water after dilution in a suction funnel on top of the tower, and the observations were repeated during a series of 3-min test periods.

During the winter of 1959–60 both the grey and the tiger shark were transferred to Pond 5 (Fig. 4), a much larger enclosure about 360 ft long and 66 ft wide. Other grey and hammerhead sharks were added to this pond; eventually

they were confined in two-thirds of its length by a fence. Observations were conducted on the shark population from the 16-ft tower which had been moved to a central location along one side. Usually the sharks would swim back and forth along the length of the enclosure in a channel which averaged about 9 ft in depth. Occasionally the tiger shark and the hammerheads (but rarely the greys) would traverse the length of the pond in shallows 1–4 ft in depth along the side of the pond opposite to the tower. Two testing techniques were employed which are henceforth referred to as “point” and “curtain-funnel” or “curtain-drum” introduction. In both, activity was recorded during the usual control and test periods in a test area 50 ft in length and extending across the width of the pond. The area, centrally located in front of the tower, was marked off by cords which stretched across the pond and were several inches above the water surface at high tide.

In “point” introduction the material was con-

tained in a 5-gal funnel on top of the tower and was introduced at a point either just below the surface or at a depth by means of a rubber tube suspended from a boom (Fig. 5). In “curtain-funnel” introduction the material passed from the funnel to a perforated hose running transversely across the bottom of the pond at the center of the test area and extending part way into the shallows. In a modification, used in the spring and summer of 1961 and called “curtain-drum” introduction, a continuous stream of salt water was pumped into the hose before and during control conditions; the stream was then switched to a 50 gal drum containing about 40 gal of sea water together with the test material. After introduction, which usually consumed about three 3-min test periods, the flow was again switched to salt water. With both methods care was taken to prevent the generation of air bubbles in the curtain for they produced a variable visual response. By using dye it was found that the curtain was fairly uniform and rela-



FIG. 4. View of Pond 5 at Hawaii Marine Laboratory showing the observation tower. (Photograph by E. S. Hobson.)

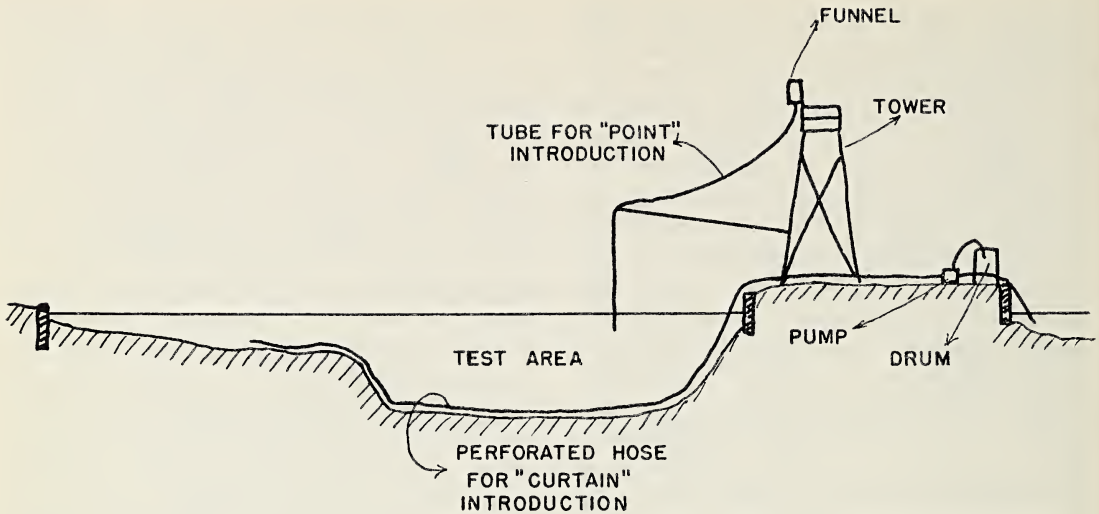


FIG. 5. Diagram of the arrangement of test apparatus in Pond 5 at Hawaii Marine Laboratory.

tively stable during periods at or near slack water. When there was a tidal current the curtain lacked uniformity in concentration and was irregular in shape; it slowly spread to one end or the other of the test area; sometimes it spread in one direction at the surface and in the opposite direction at or near the bottom. Normally the sharks would encounter the curtain of material during their passage along the deep channel. They could avoid it by swimming in the shallows.

Interpretation of a response

Based partly on quantitative data averaged as an index of activity or plotted in graphic form, partly on notes of overt responses, and, in the case of pond experiments, partly on diagrams of the swimming paths of the sharks in, out, or through the test area, the result of each experiment was classified as no noticeable response (O), sensing only (S), weak attraction (A), strong attraction (AA), weak repulsion (R), or strong repulsion (RR). Occasionally these were supplemented by other descriptions such as "startled reaction," "alarm reaction," "agitation," etc.

The category "no noticeable response" needs no further explanation. The category "sensing" was reserved for a response which consisted of a sudden start or turn on the part of the shark

on first encountering the test material but with no other noticeable component suggestive of either attraction or repulsion. Sensing responses were obtained with a variety of materials including weak acids, bases, and salts. The response was interpreted merely as an awareness of any change in the composition of an otherwise uniform environment. An "attraction" response included an initial sensing followed by a more or less prolonged hunting response, usually with rapid swimming, circling at or near the surface, and occasionally with a "gulping" or flexing of the jaws as when feeding. The shark would usually make several excited circles in the test area on encountering the material, and would then dash down the tank, returning to the test area for further circling. Almost invariably the average index of activity during test conditions was higher than during control conditions. A "repulsion" response included an initial sensing, but this was followed usually by rapid departure from the test area, a slowing of swimming speed, and a "cautious" re-approach to the test area. Often in subsequent passes the sharks would turn short of the test area. A strong repulsion was often accompanied by shaking of the head or flexing of the gill slits. Almost invariably the average index of activity during test conditions was lower than during control conditions.

Unfortunately the response to a given material varied considerably in repeated testing and was often difficult to classify. The problems of bioassay should not be minimized. The responsiveness of the sharks both at Eniwetok and Hawaii seemed to vary from day to day for unknown reasons despite our attempts to maintain standard conditions of testing and feeding. Erratic behavior, frequently encountered during both control and test conditions, in some cases could be traced to obvious sources of disturbance, such as noise, but in other cases could not be explained. Particularly exasperating was an occasionally exhibited tendency to circle at one or the other end of the pond or tank for long periods of time so that tests could not be conducted. Even though an attempt was made to conduct tests only after some reasonable uniformity in swim pattern persisted throughout control periods, there was always the question of whether or not a subtle change in behavior pattern was related to the material being tested. In classifying a response, greater reliance was placed on overt signs such as sudden turns, circling, gills flexing, and head shaking than on the quantitative data. Unfortunately the location and concentration of the material being tested was not known precisely during tests and could only be estimated from the use of dyes after an experiment had been completed. Thus even overt responses could be related to the test material only by inference.

Our caution in interpretation is reflected in the large number of responses relegated to doubtful categories in the results which follow and the numerous tests which were conducted on materials of particular interest.

RESPONSE TO EXTRACTS OF NATURAL FOODS

Experiments were conducted on the response of the tiger shark to extracts of tuna flesh and decayed shark flesh and on the response of the blacktip and grey sharks to a wide variety of potential foods including tuna, eel, grouper, snapper, parrot fish, jack, giant clam, octopus, squid, lobster, fresh shark flesh and skin, and decomposed shark flesh and skin. In general, the extracts of all food substances tested could be classed as attractants, although because of

variability in the response of the sharks sometimes several tests of the same substance were necessary to establish this conclusion. Because of this variability it was not possible to make rigorous comparisons between the attractiveness of extracts from equivalent quantities of the various foods. However, it seemed certain that extracts from moist- or oily-fleshed fish such as grouper, tuna, and eel generally resulted in greater activity than those from dry-fleshed fish such as snappers. In attempting to determine the response to nonfood substances, frequently standard extracts of grouper, tuna, or eel were used either before or after tests of the other substances to appraise the sharks' responsiveness.

From Table 1, summarizing the results of 169 tests, it will be noted that the response was classed as a strong attraction in 59, as a weak or doubtful attraction in 62, as nil or merely a sensing in 39, and as a weak or a doubtful repulsion in 9. The last, comprising 5% of the tests, warrants further comment.

The five instances of apparent repulsion in the 1959 tests at Eniwetok involved extracts of little tunny (*Euthynnus yaito*), yellowfin tuna (*Neothunnus macropterus*), and giant clam (*Tridacna*), and occurred early in the summer when testing techniques were being developed. Without doubt the response was related to either incipient pollution of the tanks or decomposition of the test materials. Excessive quantities of extracts were being used and excess food was not being removed from the tanks; one or both of these factors resulted in the death of several sharks in one compartment before the condition was rectified. Our notes state that the tunny extract, which had been kept for 9 days, smelt foul.

The four instances of apparent repulsion in the 1960 tests, involving standard extracts of eel, again took place early in the summer and involved not pollution of the tanks but decomposition of the extract even though it was held at ice-box temperature. The extract was prepared on July 7, 1960. On that and the following day tests of both greys and blacktips showed strong attraction (Figure 6A). On July 13, in seven tests the responses were indicated as weak or questionable attraction, sensing only, or nil. On July 16, the material produced erratic re-

TABLE 1

RESPONSE OF SHARKS TO EXTRACTS OF NATURAL FOOD AT HAWAII MARINE LABORATORY (HML)
AND ENIWETOK MARINE LABORATORY (EMBL)

YEAR	SHARKS, LABORATORY, AND MATERIAL	RESPONSE*					Total
		RR	R-R?	O-S	A-A?	AA	
1959	Tiger, HML						
	Fresh tuna extract	—	—	3	2	2	7
1959	Aged shark extract	—	—	—	1	1	2
	Blacktips, EMBL						
	Various extracts	—	5	21	32	32	90
1960	Aged shark extract	—	—	7	8	3	18
	Blacktips and greys, EMBL						
	Fresh extracts	—	—	—	12	18	30
	Aged eel extract	—	4	8	6	2	20
	Aged shark extract	—	—	—	1	1	2
Total		—	9	39	62	59	169

* RR, strong repulsion; R-R?, weak or doubtful repulsion; O-S, no apparent response or sensing; A-A?, weak or doubtful attraction; AA, strong attraction.

sponses, some of which were classed as doubtful repulsion. The notes indicated that the material smelt foul. Similar results were obtained with the same material on July 18. The sharks were tested with freshly prepared standard eel extract on July 20 and both species showed a strong attraction response.

In direct contrast to the above results are those with extracts of decayed shark flesh, which after a week in the hot sun smelt particularly foul. Our material consisted of extract of decayed hammerhead and of decayed tiger shark tested on the tiger shark at the Hawaii Laboratory (two tests) and of extracts of decayed blacktip shark flesh and skin tested on blacktip sharks at Eniwetok (five tests). In addition, we tested blacktips at Eniwetok on an alleged shark repellent, supplied by a fisherman, which contained extract of decayed shark flesh as the principle component (six tests). We also tested fractions of extract of decomposed shark flesh which were supplied by Dr. M. A. Steinberg, Bureau of Commercial Fisheries Technological Laboratory, Gloucester, Mass. (11 tests). No repellent effects were noted in any of the tests. On the contrary, the majority yielded responses which were classed as either weak or strong attraction. Our results with the fractions of extract were in agreement with those reported by Steinberg (1960) when his material was later tested on the lemon shark (*Negaprion brevirostris*), the

reef shark (*Carcharhinus falciformis*), and the bull shark (*Carcharhinus leucas*) at the Lerner Marine Laboratory, Bimini, Bahamas, B. W. I.

Our results with extracts of decomposed shark flesh seem to be at variance with those of Springer (1955), who found that the feeding of the dogshark (*Mustelus canis*) was consistently inhibited by the presence of decayed shark flesh. Although several hypotheses might be formulated to account for the difference in results, no convincing explanation can be made at the present time, particularly in view of the apparent repulsion noted with decomposed eel and other extracts noted in preceding paragraphs.

BEHAVIOR OF STARVED SHARKS

In considering shark predation, the questions arise as to how long a shark can exist without food and whether its olfactory response is modified by starvation. Some information on these points was obtained for small sharks at the Eniwetok laboratory.

In 1959, following the summer's work, AEC personnel at Eniwetok volunteered to keep track of the fate of four small blacktips under starvation conditions. Three of the sharks died after about 2 months in captivity. One survived for 3 months but it was not known to what extent it had maintained itself by feeding on the sharks which had died.

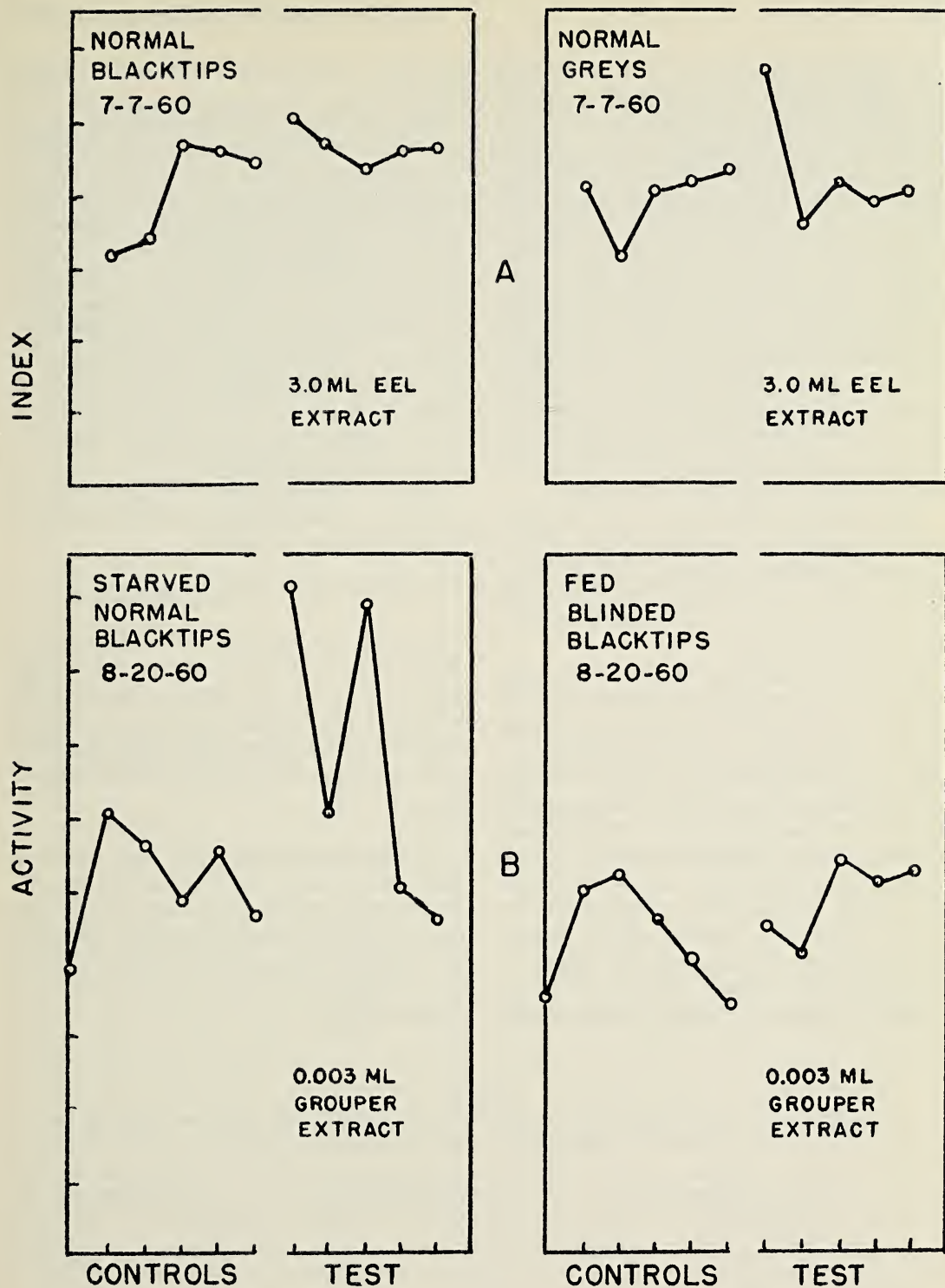


FIG. 6. Activity index during successive 2-min periods, illustrating (A) response of blacktip and grey sharks to standard eel extract, and (B) response of starved (normal) and fed (blinded) blacktip sharks to a 1/1000 dilution of standard grouper extract.

In 1960, four blacktip and four grey sharks were starved under close supervision. Of the blacktips, a 20-inch male died after 36 days, a 28-inch female died after 40 days, a 20-inch female died after 40 days and a 27-inch female survived for 43 days and was then fed. Of the greys, a 28-inch female died after 32 days and a 36-inch male died after 40 days. Two 30-inch females were starved respectively for 34 and 46 days and were then fed. During starvation, the sharks became very thin. Those which died had difficulty in maintaining their equilibrium for several hours before death; they could not be revived by forced feeding. These experiments show that small blacktip and grey sharks can survive for more than a month without food but that some will die after 5 or 6 weeks.

Using standard extract, tests were run at intervals to measure the response activity of both the starved blacktips and greys and, for comparison, that of four blinded blacktips which were fed two or three times a week. Activity data are given in Table 2.

The activity index for the fed sharks fluctuated from day to day but showed no trend. In contrast, the index for the starved sharks showed a more or less steady increase during both control and test conditions, particularly in the case of the blacktips. For the latter, the decrease in index on the last day is due to the moribund condition of two of the four sharks. As starvation proceeded, the sharks seemed to become increasingly restless and to respond with increasing vigor to the standard extract. Tests on the greys were discontinued after August 5, 1961 because of the death of one shark and the moribund condition of another (starvation be-

gan about 2 weeks earlier than with the blacktips).

Normally the blinded blacktips were more sensitive to odorous substances than the blacktips with normal vision. This situation was reversed when the latter sharks were starved. This is illustrated by one experiment (August 20, 1960) when both the blind, fed and the normal, starved sharks were tested with a 1/1000 dilution of standard extract (Fig. 6B). Using 0.003 ml (rather than the usual 3.0 ml) the fed sharks showed a weak attraction response which did not differ greatly from mere sensing. The starved blacktips on the other hand gave a strong attraction response which included the usual excited circling and hunting activity.

There is no doubt that hungry sharks are much more responsive than fed sharks to minute traces of odorous substances.

RESPONSE TO HUMAN MATERIALS

In this section are reported the results of tests on the response of normal and blinded blacktip sharks and normal grey sharks to human urine, blood and sweat, and to L-serine, a presumed component of human sweat. Other materials such as faeces and vomit were not investigated.

Urine

At Eniwetok, in both 1959 (eight tests) and 1960 (three tests) blacktip sharks were presented with human urine in quantities ranging from 3 to 80 ml of whole material. The urine was sensed, as indicated by a swirl or turn on encountering it, but there was no other consistent response.

TABLE 2
ACTIVITY INDEX OF FED (BLIND) AND STARVED (NORMAL) SHARKS TO STANDARD EXTRACT AT
ENIWETOK MARINE BIOLOGICAL LABORATORY, 1960

DATE	FED BLACKTIPS		STARVED BLACKTIPS		STARVED GREYS	
	Controls	Test	Controls	Test	Controls	Test
7/20	29.2	41.2	31.0	40.4	33.8	60.4
7/23	21.2	32.0	31.8	44.2	23.8	38.6
7/29	34.8	37.6	57.4	76.8	52.6	74.2
8/5	29.6	54.0	50.6	71.2	86.3	96.8
8/18	27.2	36.2	56.0	97.0	—	—
8/25	23.4	32.2	36.4	49.2	—	—

TABLE 3
RESPONSE OF SHARKS AT ENIWETOK MARINE BIOLOGICAL LABORATORY TO HUMAN BLOOD

YEAR	MATERIAL AND SHARKS	RESPONSE*					
		RR	R-R?	O-S	A-A?	AA	Total
1959	Fresh or aged blood	—	4	4	1	—	9
	Normal blacktips	1	4	2	2	—	9
	Blinded blacktips	1	8	6	3	—	18
	Total						
1960	Aged blood (4–6 days)						
	Normal blacktips	1	2	1	—	—	4
	Blinded blacktips	—	2	3	—	—	5
	Normal greys	—	—	1	4	—	5
	Total	1	4	5	4	—	14
1960	Fresh blood (1–2 days)						
	Normal blacktips	—	—	2	2	2	6
	Blinded blacktips	—	—	2	2	3	7
	Normal greys	—	—	1	4	—	5
	Total	—	—	5	8	5	18

* RR, strong repulsion; R-R?, weak or doubtful repulsion; O-S, no apparent response or sensing; A-A?, weak or doubtful attraction; AA, strong attraction.

Blood

Most authors agree that blood in the water excites sharks. For example, Whitely (1940) notes that small blacktip sharks on the Great Barrier Reef would follow persons who had scratched their legs on coral and would dog their footsteps through slightly bloodied water. Bigelow and Schroeder (1948) remark that if persons in the water are bleeding from injuries the danger from shark attack may be imminent and the results may prove fatal. Moreover, they state that the more voracious of the larger sharks are excited by blood in the water to such a degree that they will make ferocious attacks whether the object be fish, whales, or man, dead or alive. In contrast, based on experience with releasing turtle and sheep blood while fishing for sharks, Wright (1948) concluded on admittedly weak evidence that blood alone, without the presence of some moving object, did not release the attack pattern. Steinberg (1961) reports that a captive lemon shark was not attracted by solution of dried beef blood.

The results of experiments with human blood in 1959 are included in Table 3. The responses were much more variable and erratic than those with food extract. A sensing was at times fol-

lowed by an attraction response and at other times by an apparent flight reaction and a tendency to avoid the test area. The erratic behavior was unlikely related to a visual stimulus as it occurred in both the blinded sharks and those with normal vision. Moreover the quantities used, even when the techniques were being developed, were not sufficient to produce noticeable coloration in the water. It was suspected that the variability in response was related to the freshness of the blood.

In 1960, 32 experiments were conducted with human blood. The results are summarized in Table 3 and are given in detail in Table 7. Quantities ranged from 0.03 to 6.0 ml of a suspension of 5 ml of whole blood in 250 ml of sea water. With fresh blood tested within 1 or 2 days after collection, 3.0 ml of the suspension usually produced a moderate or strong attraction response with the usual behavior components: excited circling, swirling and hunting. An attraction response was obtained with 0.3 ml of the fresh suspension on several occasions and with as little as 0.03 ml in one test. By the use of dye it was estimated that the shark first encountered the material when it had mixed with 1/4 to 1/2 of the volume of the test compartment. If this dilution is assumed, it may be estimated

that the sharks were attracted to human blood at a concentration of about 0.1 to 0.01 parts per million of sea water.

A blood suspension held under refrigeration for 4 days or longer usually underwent hemolysis and acquired a faint to strong putrid odor. The aged blood produced erratic results with blacktip sharks as had been suspected in the 1959 tests. At times there was only a sensing of the material, an avoidance of the area, or possibly a slight attraction. At other times there seemed to be a "startled" or "alarm" reaction with speeding from the area such as had been noticed the previous year. This was classed as repulsion. With grey sharks, on the other hand, the hemolyzed blood seemed more consistently attractive.

Our results prove that fresh blood excites blacktip and grey sharks and promotes a strong hunting response. They suggest that decomposed human blood contains a component which is repellent to blacktips.

Sweat

A large number of experiments were conducted at both the Eniwetok and the Hawaii

laboratories on the response of sharks to human sweat. They were stimulated by the observation of Brett and McKinnon (1954) that water in which human hands had been rinsed retarded the upstream migration of salmon and induced an "alarm" response.

Sweat was collected initially by sponging the body and wringing the sponge in 500 ml of sea water. Later, at Eniwetok it was collected directly from the body as it ran down arms, chest and abdomen in the hot, humid atmosphere of the shark house, and at Hawaii it was collected in the same way by exercising and subjecting the body to heat lamps. The material was tested according to the standard procedures already described. Each sweat test was usually followed or preceded by standard extract to appraise the sharks' responsiveness to a known attractant.

The results of 29 tests conducted on normal and blinded blacktip sharks at Eniwetok are included in summary form in Table 4 and are given in detail in Table 8. The majority of the tests yielded results which were classed as repulsion. A weak repellent effect (R) was comprised of an initial sensing, followed by a slowing of swimming speed, an apparent wariness,

TABLE 4

RESPONSE OF SHARKS TO HUMAN SWEAT AT ENIWETOK MARINE BIOLOGICAL LABORATORY (EMBL) AND HAWAII MARINE LABORATORY (HML)

YEAR	LABORATORY AND SHARKS	RESPONSE*					
		RR	R-R?	O-S	A-A?	AA	Total
1959	EMBL, Normal blacktips	1	6	3	1	—	11
	Blinded blacktips	8	9	1	—	—	18
	Total	9	15	4	1	—	29
1960	EMBL, Normal blacktips	5	7	1	1	—	14
	Blinded blacktips	2	4	1	—	—	7
	EMBL, Normal greys	—	9	6	—	—	15
	Total	7	20	8	1	—	36
1959-60	HML, tiger, Pond 2	1	3	2	—	—	6
	HML, tiger, grey, hammerhead, Pond 5	—	8	7	—	—	15
	Total	1	11	9	—	—	21
1960-61	HML, tiger, greys, Pond 5	—	3	2	—	—	5
Total		17	49	23	2	—	91

* RR, strong repulsion; R-R?, weak or doubtful repulsion; O-S, no apparent response or sensing; A-A?, weak or doubtful attraction; AA, strong attraction.

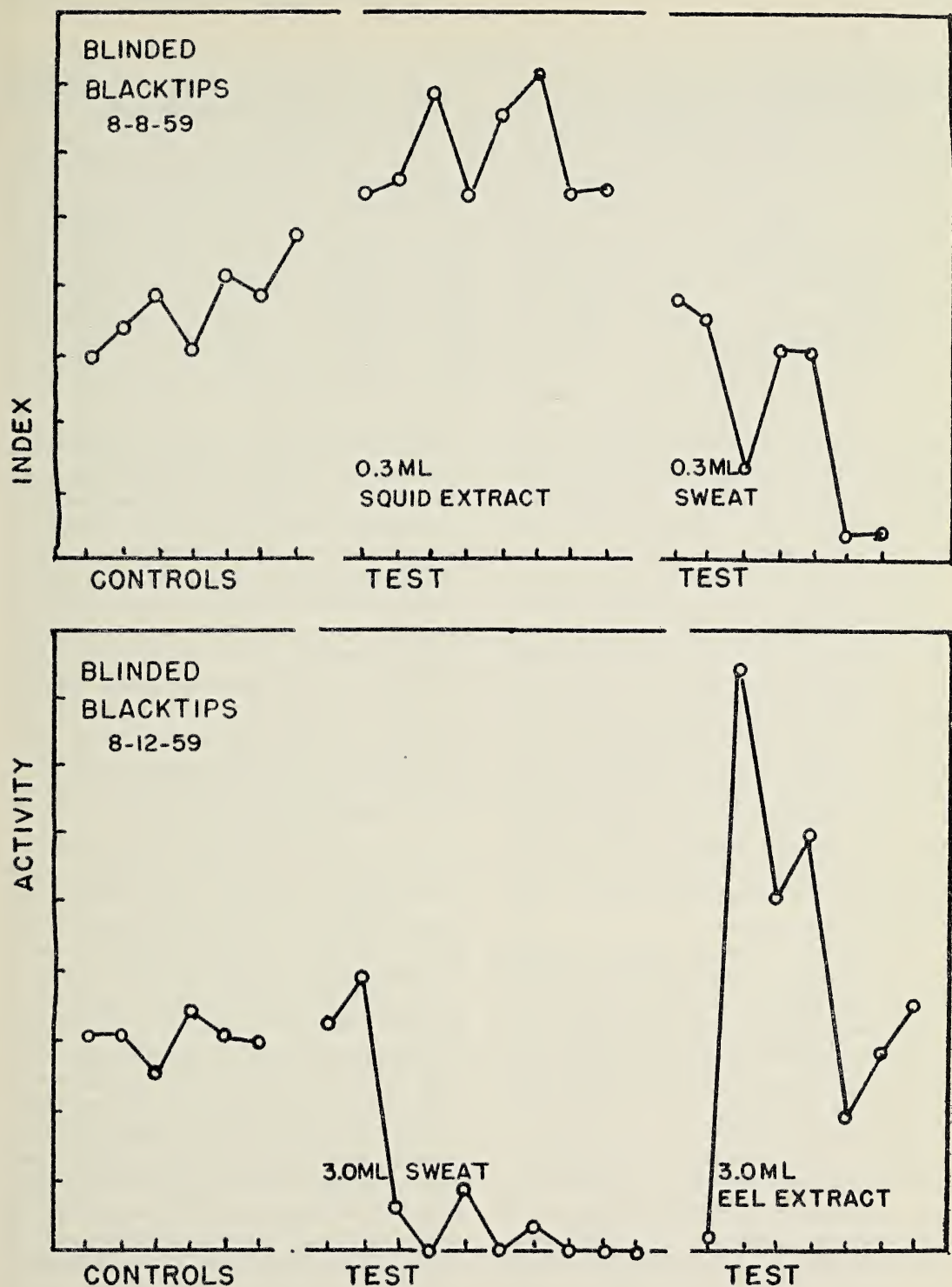


FIG. 7. Activity index during successive 2-min periods in two experiments, illustrating the difference in response of blinded blacktip sharks to human sweat and to food extract.

TABLE 5

INDEX OF ACTIVITY IN SUCCESSIVE RINGS (NO. 1, CENTER) OF A TARGET AREA FOR A HAMMERHEAD SHARK DURING SUCCESSIVE TESTS OF "TILAPIA WATER" AND HUMAN SWEAT IN POND 5, HAWAII MARINE LABORATORY, JUNE 16, 1960

TEST	RING NUMBER				AVERAGE
	1	2	3	4	
Controls, sea water	4.5	5.5	14.8	20.7	11.4
Tilapia water	27.3	29.3	22.0	11.8	22.6
Sweat	5.4	8.3	13.1	12.3	9.8
Tilapia water	28.4	36.8	29.4	20.6	28.8
Controls, sea water	15.0	19.1	16.9	20.0	17.7
Tilapia water plus sweat	15.1	30.0	21.2	16.9	20.8

and a tendency to avoid the test area. A strong repellent effect (RR) included in addition a rapid exit from the area following sensing, sometimes accompanied by head shaking. When no noticeable response occurred it was found usually that this was also the case with the known attractant. In the one case classed as doubtful attraction, the first sweat test which was conducted, it is likely that initial sensing was interpreted as attraction. The quantitative data of Table 8, illustrated for two experiments in Figure 7, give convincing evidence of a depression of shark activity following the introduction of sweat. In each of the 29 tests, the time spent in the test areas during test conditions was less than during control conditions; this is in striking contrast to the results with standard extract where the reverse is almost invariably encountered.

The apparent aversion to sweat was exhibited by both normal and blinded blacktips, possibly to a greater extent in the latter. The sweat of one donor (ALT) seemed to be effective at a roughly-calculated concentration of about 1 part per million. The sweat of a second donor (TAP) produced no obvious repellent effects in the two tests which were made.

Because of the possibility that the sharks in 1959 had become conditioned to associate sweat with punishment, e.g., from handling, the experiments were repeated during 1960, taking precautions against sweat dripping accidentally into the water and using fresh sharks, some of which had not been touched by hand. The results in 1960 were similar to those in 1959 (Tables 4, 9). With the blacktips the majority

of the responses were classed as repulsion; in the one case of apparent attraction, again the first test of the season, the sharks had just been introduced and still exhibited erratic behavior. There was no noticeable difference in response between the blinded and normal blacktips. With the grey sharks an aversion to human sweat was present in the majority of the tests but it seemed less pronounced than with the blacktips. There were no obvious differences in response between the sweat of three donors. The sweat did not decrease in potency with aging at room temperature for several days; rather, its repellent properties seemed to increase but this could not be established with certainty.

In tests conducted during the winter of 1959-60 on the tiger, hammerhead, and grey sharks at the Hawaii laboratory, larger quantities of sweat (10-40 ml) were used because of the greater volume of the ponds compared with the Eniwetok tanks. In most cases the results, summarized in Table 4, showed vague repellent effects following the introduction of sweat. For the most part, the sharks displayed only a tendency to avoid the test area (R?), occasionally with a sharp veering from the presumed location of the material and rapid swimming through or away from the test area (R). Apart from these latter overt responses which were displayed on occasion by all three species, the only strong repulsion concerned the tiger shark in one test and consisted of obvious "agitation" and head shaking. Repellent effects were noted with the sweat of all three donors (ALT, RJ, and ESH) but more consistently with that of the first two than the last.

A different technique was employed in tests with the hammerhead which was particularly responsive to attractants. The introduction hose running from the funnel on top of the tower was submerged just below the surface at the center of a bullseye target area 32 ft in diameter, the boundaries of which were judged by eye from reference points on the bottom. During control conditions, sea water was introduced from the funnel. During test conditions the following materials were used in varied sequence: (1) an attractant consisting of water from the funnel in which fish (*Tilapia*) were swimming, (2) 50 ml of sweat mixed with sea water in the funnel, and (3) a mixture of the attractant and sweat in sea water. Activity data on one test are given in Table 5. Based on records of the time spent and the path followed by the shark in the target area, activity was calculated as the distance swum in each of four rings of the target per unit of time. It is apparent that, in general, activity was greatest with the attractant, intermediate with the mixture of sweat and attractant, and least (less than controls) with sweat alone. The sweat depressed but did not eliminate the response to the attractant.

By tracing the spread of materials in the pond with the use of dye and calculating the volume of sea water involved, it was concluded that the actual sea water concentration of sweat in the pond experiments at the Hawaii laboratory were still considerably less than those used in the tank experiments at Eniwetok. Additional experiments were undertaken during the early summer of 1961 using much larger quantities of sweat (100–400 ml per test) and the improved "curtain-drum" method of introduction. The results are summarized in Table 4. Despite the larger quantities of sweat which were used no strong repulsion was noted. In the five tests, there was weak or doubtful repulsion in three and sensing only in two. In those tests indicating repulsion, all three species of sharks, especially the tiger, showed definite signs of aversion including veering from the curtain and gill flexing. The sweat of one donor (SK) seemed to be more active than that of the other (BLO).

From the above experiments on blacktip, grey, tiger, and hammerhead sharks one cannot conclude that human sweat, per se, is an active shark repellent. On the other hand, it is certain

that human sweat does contain, at least at times, a component which is aversive to sharks. Occasionally this induces overt signs of repulsion such as head shaking, gill flexing, veering, and rapid retreat; more frequently it induces only a subtle wariness manifested chiefly by avoidance of the area of introduction. The response is highly variable. This is unfortunate but almost inevitable when one considers the uncontrolled environmental conditions and the many factors which could contribute to both the variability of shark behavior and variability of sweat composition.

Steinberg (1961) found no evidence of repellent properties in either human sweat or pure compounds forming constituents of human sweat in tests with a captive lemon shark at the Lerner Marine Laboratory. Unfortunately he gives no information on the concentrations of material used. Moreover, he reports that the lemon shark was not responsive to solutions of dried beef blood nor would it eat chunks of fresh shark liver which, at other times, had been particularly attractive to captive sharks. His negative results are understandable. It has been our experience that sharks which have not yet fed in captivity do not respond to either highly attractive substances such as eel extract or fresh human blood, nor do they respond to subtle repellent substances such as human sweat.

In view of the results of this series of tests, it seems safe to assume that shark attack on humans is not motivated by the smell of human sweat.

L-serine

Following the discovery by Brett and McKinnon (1954) that human hand rinse retarded the migration of salmon, Idler, Fagerlund, and Mayoh (1956) undertook an analysis of hand rinse to determine the repellent component(s). By employing various fractionation techniques and testing the fractions on migrating salmon, they were able to identify the active fractions as amino acids of which serine was a major component. In further tests, the L-isomer of serine was found to induce the alarm response whereas D-isomer did not. They stated "L-serine definitely elicited a typical alarm reaction but the effects were neither so dramatic nor so long a duration as the response obtained by hand

rinse." As hand rinse doubtless contained sweat and as sweat produced a repellent effect on sharks, it was decided to investigate their response to L-serine.

Three tests were conducted at the Hawaii laboratory on the tiger shark in Pond 2, during the winter of 1959-60, using 1.0 gm of L-serine per test. In the first, there was no overt response except an obvious sensing on encountering the material. In the second, the shark showed a sensing of the material, followed by rapid exits from the area and violent head shaking. In the third test, there was no noticeable response. In all three, however, the time spent in the test area during test conditions was less than during controls, as had also been the case with sweat.

Three tests were conducted on blacktip sharks at the Eniwetok laboratory in 1960, using 6 ml of a solution containing 1.0 gm of L-serine (i.e., 0.12 gm per test). No repellent effects were noted other than a "wariness" in one test. Again, however, the time spent in the test area during test conditions was less than during controls.

As definite repellent results had been noted in one test with the tiger shark, it was decided to run a third series at the Hawaii laboratory during the summer of 1961, using much larger quantities of L-serine despite its high cost. Three tests were conducted on the tiger and grey sharks co-inhabiting Pond 5, using the "curtain-drum" technique.

In all three tests the tiger shark displayed an aversion to the chemical but only after introduction of the material had been completed. Introduction required about 10 min (three to four 3-min periods). It seemed either that the response occurred after a threshold concentration of the material had been reached, or that there was a latent period between exposure to the material and response. The overt response was a violent head shaking either while in or while leaving the area of concentration. At times this took place at the surface and caused considerable splashing. However, in only the first test (25 gm L-serine) was there frequent rapid exit from the area on encountering the material. In the second test (50 gm L-serine) there was swerving and head shaking after encountering the material, but no turning-back on initial encounter. The response was less pro-

nounced than in the first test even though twice the quantity of material had been used. This may have been due to a higher tide and thus a larger volume of water and greater dilution of the material despite the larger quantity used. The shark frequently avoided the material by swimming in the shallows on the far side of the pond. In the third test (25 gm L-serine plus 10 ml of a 99% nicotine solution), the tiger shark again displayed agitation and head shaking. The response, however, occurred less frequently than in the other two experiments. The nicotine had been added in the hope of a synergistic effect; it had been our impression that the sweat of smokers was more repellent to the sharks than that of nonsmokers. Possibly it tended to inhibit rather than increase the effect of L-serine.

The grey sharks, in contrast to the tiger shark, were not obviously agitated by L-serine; no head shaking or gill flexing was observed. In the first test, two grey sharks of the same species veered sharply on first encountering the material and returned to the end of the pond. Thereafter all three grey sharks circled in the end zone for the duration of the experiment. In the second test no veering was noted but there was repeated circling in the end zone. It was uncertain whether this could be interpreted as a repellent effect, for the same habit was noted occasionally during control periods. In the third test, all three grey sharks passed through the test area without signs of awareness, agitation, or repulsion.

Although there is no doubt that the tiger shark was actively repelled by L-serine, the physiological mechanism producing the response is unknown. We can offer no satisfactory explanation of the difference in response of the tiger and the greys to L-serine. It may have involved species differences in physiological effect or differences in the concentration of materials to which they were subjected. The latter is possible even though the tests were conducted simultaneously on the tiger and the greys, for uneven curtains of material were formed by tidal currents in all three tests and the shallow-swimming tiger shark may have encountered different concentrations than the deep-swimming grey sharks. It may be added, however, that directly opposite results were obtained with a highly irritating lachrimator which is presently

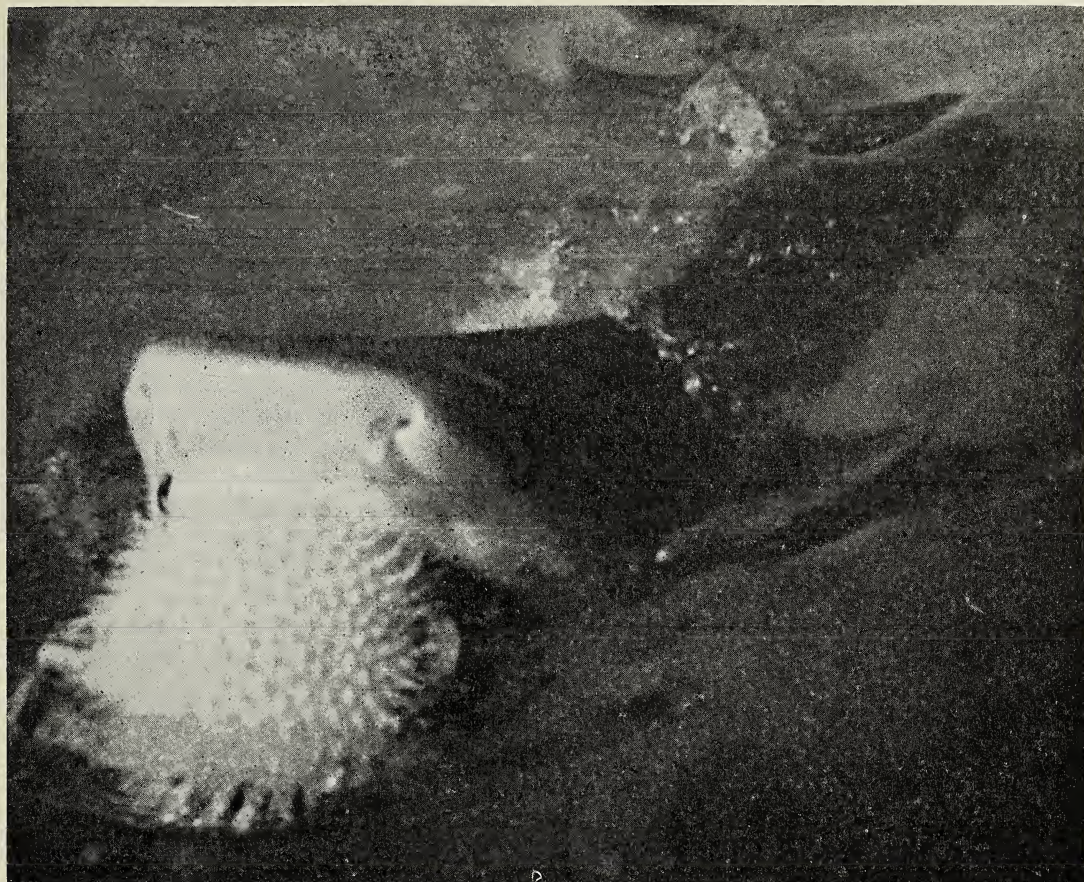


FIG. 8. View of a tiger shark attempting to swallow a spiny puffer. (Photograph by E. S. Hobson.)

being tested as a potential shark repellent. With this substance, the greys responded violently with gill flexing, head shaking, and definite avoidance of the curtain. The tiger shark, on the other hand, was not noticeably affected until the concentration of the material had been doubled.

In the foregoing sections it has been shown that certain species of sharks have an aversion to and at times are repelled by aged food extracts, aged human blood, fresh or aged human sweat, and finally L-serine. Serine, presumably the D-isomer, is a common amino acid in both foodstuffs and blood. It may be hypothesized that at least one of the repelling substances in all of the above materials is L-serine, which is presumably present as the L-isomer in human sweat, but which may be formed in foodstuffs

and blood from the nonrepellent D-isomer during decomposition.

It has *not* been demonstrated that L-serine has sufficiently active repellent properties to deter shark attack on prey, including man. However its repellent properties, its presence in human sweat, and its possible generation during the decomposition of foodstuffs and blood warrant further investigation.

RESPONSE TO LIVING FISH

Although at times sharks may obtain a large portion of their food by scavenging dead materials, they also feed on living prey. When the prey is wounded, the sharks are doubtless attracted by the odor of body juices as well as by visual and possibly by other stimuli. It is

reasonably certain that most species also attack healthy, undamaged, living prey, although apart from attack on man, observations of feeding activity are singularly lacking in the literature.

In the summer of 1959, a group of biologists from the Hawaii Marine Laboratory witnessed the persistent attack of a tiger shark on a spiny puffer which had inflated itself and was floating at the surface in Kaneohe Bay. The shark's attempts to swallow the puffer (Fig. 8) lasted for about 10 min despite the presence of the observers who circled in an outboard motor boat. During the shark's slow, awkward passes at the puffer the sound of its jaws clamping together as it missed the prey could be heard.

Other species of sharks are capable of catching fast moving prey. For example, Eibl-Eibesfeldt and Hass (1959) observed both the grey shark (*Carcharhinus menisorrhoea*) and the blacktip (*C. melanopterus*) actively feeding on healthy fish in the Indian Ocean, and even herding them against the shoreline to facilitate capture.

Although vision is doubtless the predominant sense which is used by sharks on converging on living undamaged prey, it is possible that olfaction may also be involved. I have found only one observation in the literature which supports this possibility, that reported by Sheldon (1911) and again by Parker and Sheldon (1913), who found that the dogshark (*Mustelus*

canis) was able to locate undamaged living crabs concealed in a wrapping of eelgrass. The response of sharks to living, presumably undamaged fish was investigated at both the Eniwetok and the Hawaii laboratories.

Results

In one series of experiments at Eniwetok in 1959, an empty wire cage (about $6 \times 6 \times 12$ inches) was silently lowered to the bottom of a test area at the upstream end of a compartment containing four blinded blacktip sharks. After the usual series of control periods during which activity was recorded, the cage was removed, a living fish was added, and it was again lowered into the test area when the sharks were at the far end of the compartment. Activity was again observed during a series of test periods. The water flow was maintained during both control and test conditions.

The results are included in Table 6. In most of the experiments attraction responses were obtained with a 12-inch grouper (*Epinephalus fuscoguttatus*), an 8-inch squirrel fish (Holo-centridae), and an 8-inch stone fish (*Synancaja verrucosa*). Although probably excited by confinement in the cage, the fish did not move about much after the cage had been lowered. There was often a delay of several test periods before the sharks showed any response. Then, in most of the experiments, one or more sharks suddenly

TABLE 6
RESPONSE OF SHARKS AT ENIWETOK MARINE BIOLOGICAL LABORATORY TO LIVING FISH, 1959

SHARKS AND FISH	RESPONSE*					Total
	RR	R-R?	O-S	A-A?	AA	
Blinded blacktips						
Caged grouper	—	—	1	3	1	5
Caged squirrel fish	—	—	1	1	2	4
Caged stonefish	—	—	—	2	—	2
Total	—	—	2	6	3	11
Blinded blacktips						
Grouper water, grouper present	—	—	1	2	2	5
Grouper water, grouper absent	—	—	2	—	1	3
Eel water, eel present	—	—	—	1	—	1
Blacktip water, blacktip absent	—	—	2	—	—	2
Total	—	—	5	3	3	11

* RR, strong repulsion; R-R?, weak or doubtful repulsion; O-S, no apparent response or sensing; A-A?, weak or doubtful attraction; AA, strong attraction.

TABLE 7

RESPONSE OF NORMAL BLACKTIP SHARKS (NB), BLINDED BLACKTIP SHARKS (BB), AND NORMAL GREY SHARKS (NG) TO HUMAN BLOOD AT ENIWETOK LABORATORY, 1960

DATE (1960)	TIME	TANK	SHARKS	BLOOD (ML)	DONOR, DATE	ACTIVITY INDEX		RESPONSE*
						Controls	Test	
7/12	0954	I (F-I)	2BB	3.0	JK 7/8	26.0	9.0	R
	1040	II (A-C)	2NG	3.0	JK 7/8	13.0	20.2	A
	1108	I (A-D)	2NB	3.0	JK 7/8	57.8	39.0	R
	1445	I (F-I)	2BB	6.0	JK 7/8	21.6	6.6	R
	1515	II (A-C)	2NG	6.0	JK 7/8	19.8	24.6	A
	1540	I (A-D)	2NB	6.0	JK 7/8	15.6	13.2	R?
7/18	1529	I (F-I)	2BB	3.0	JK 7/8	21.6	24.6	O?
	1552	I (A-D)	2NB	3.0	JK 7/8	37.2	17.8	RR
	1645	II (A-C)	2NG	3.0	JK 7/8	11.0	10.0	O?
7/21	1015	I (F-I)	4BB	3.0	ALT 7/20	22.8	35.6	AA
	1045	I (A-D)	4NB	3.0	ALT 7/20	27.7	26.4	O?
	1135	II (A-C)	4NG	3.0	ALT 7/20	37.4	49.8	A
	1350	I (F-I)	4BB	3.0	ALT 7/20	30.4	39.2	AA
	1415	I (A-D)	4NB	3.0	ALT 7/20	21.8	28.0	A
	1450	II (A-C)	4NG	3.0	ALT 7/20	33.7	44.2	A
7/22	1015	I (F-I)	4BB	0.3	ALT 7/20	26.4	41.6	AA
	1045	I (A-D)	4NB	0.3	ALT 7/20	31.6	40.0	AA
	1135	II (A-C)	4NG	0.3	ALT 7/20	24.6	35.2	A
	1405	I (F-I)	4BB	0.03	ALT 7/20	30.6	35.0	A
7/26	0910	I (F-I)	4BB	3.0	ALT 7/20	22.8	25.0	O?
	1000	I (A-D)	4NB	3.0	ALT 7/20	51.0	46.4	O?
	1135	II (A-C)	4NG	3.0	ALT 7/20	28.9	40.8	A
	2035	I (F-I)	4BB	3.0	ALT 7/20	34.6	36.8	O
	2150	II (A-C)	4NG	3.0	ALT 7/20	31.0	36.8	A
7/27	0925	I (F-I)	4BB	0.3	SK 7/26	23.6	27.6	O
				1.0	SK 7/26	—	22.6	O
				3.0	SK 7/26	—	31.8	A
				0.3	SK 7/26	45.6	46.2	O
				1.0	SK 7/26	—	56.0	A
	1045	I (A-D)	4NB	3.0	SK 7/26	—	57.2	AA
				1.0	SK 7/26	—	53.2	O
				3.0	SK 7/27	—	52.2	A
	1500	II (A-C)	4NG	1.0				
				3.0				

* RR, strong repulsion; R, weak repulsion; O, no apparent response except sensing; A, weak attraction; AA, strong attraction.

became excited and engaged in the typical hunting response. It is assumed that they were stimulated by odors emanating from the fish. In view of the delayed response, it seems unlikely that the blinded sharks were attracted by vibrations or sounds that may have been made by the fish although this possibility could not be ruled out in these rather crude experiments.

In another series of experiments at Eniwetok in 1959, an uninjured fish was held in a bucket of saltwater for 15 to 20 min prior to an experiment. The bucket was slapped or agitated

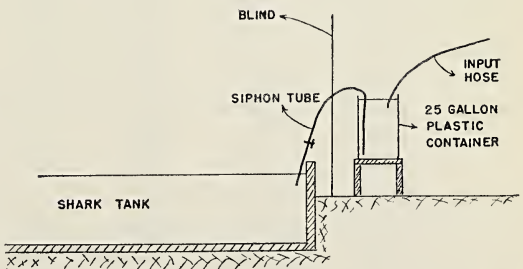


FIG. 9. Diagram of apparatus used at Eniwetok Marine Biological Laboratory for investigating response of sharks to living fish.

to keep the fish in an excited state. During control conditions, water from another bucket of sea water was siphoned into the test area of the compartment containing the four blinded blacktip sharks. The siphon was then switched to the bucket of water which either contained the fish or from which the fish had been removed. The usual observations were made during a series of control and test periods.

The results are included in Table 6. The

blinded blacktip sharks showed an attraction response in most of the experiments with the "grouper water" and in the one experiment with "eel water" (*Gymnothorax*). It was concluded that the water in which these fish had been confined contained some substance which was attractive to the sharks. The blinded blacktips did not show a noticeable attraction response to "blacktip water."

During the winter of 1959-60 similar ex-

TABLE 8
RESPONSE OF NORMAL BLACKTIP SHARKS (NB) AND BLINDED BLACKTIP SHARKS (BB) TO
HUMAN SWEAT AT ENIWETOK LABORATORY, 1959

DATE (1959)	TIME	TANK	SHARKS	SWEAT (ML)	DONOR, DATE	ACTIVITY INDEX		RESPONSE*
						Controls	Test	
8/8	1905	I (A-D)	3NB	0.3	ALT 8/8†	97.7	65.9	A?
	1930	I (A-D)	3NB	0.3	ALT 8/8†	—	73.7	R
	2115	I (F-I)	3BB	0.3	ALT 8/8†	67.6	52.7	R
8/9	1800	I (F-I)	2BB	3.0	ALT 8/8†	29.4	14.1	RR
	1945	I (A-D)	2NB	3.0	ALT 8/8†	54.4	41.7	R
8/10	0845	I (A-D)	2NB	3.0	ALT 8/8†	54.0	52.2	O
	0925	I (F-I)	2BB	3.0	ALT 8/8†	45.0	26.8	R
8/11	2322	I (F-I)	2BB	2-3	TAP 8/11	39.4	25.0	O?
8/12	0035	I (A-D)	2NB	2-3	TAP 8/11	70.0	58.8	O?
	1910	I (F-I)	2BB	3.0	ALT 8/8†	29.5	9.3	RR
	2010	I (A-D)	2NB	3.0	ALT 8/8†	73.6	61.9	R
8/13	1553	I (F-I)	2BB	3.0	ALT 8/8†	33.0	5.9	RR
	1710	I (A-D)	2NB	3.0	ALT 8/8†	68.2	58.5	R
8/14	1905	I (F-I)	2BB	3.0	ALT 8/14	54.0	35.3	RR
	2025	I (A-D)	2NB	3.0	ALT 8/14	67.0	57.7	R
8/16	1900	I (A-D)	2NB	0.06	ALT 8/14	80.8	77.8	O
	1930	I (A-D)	2NB	3.0	ALT 8/14	—	74.2	R?
	2010	I (F-I)	2BB	3.0	ALT 8/14	9.2	5.7	R
8/18	1355	I (A-D)	2NB	50.0	ALT 8/8†	34.8	17.5	RR
8/24	2010	II (G-I)	4BB	10.0	ALT 8/8†	85.7	56.3	RR
8/25	1515	II (G-I)	1BB	10.0	ALT 8/8†	24.2	1.9	RR
8/31	1930	I (F-I)	2BB	3.0	ALT 8/31	26.9	12.2	RR
9/1	2155	I (F-I)	2BB	3.0	ALT 8/31	37.0	32.0	R
9/3	1450	I (F-I)	3BB	3.0	ALT 8/8†	38.6	13.5	RR
	1900	I (F-I)	3BB	3.0	ALT 8/8†	53.0	36.0	R
	2145	I (F-I)	3BB	3.0	ALT 8/8†	49.6	35.2	R
9/4	1930	I (F-I)	2BB	3.0	ALT 9/4	37.0	24.2	R
	2145	I (F-I)	2BB	3.0	ALT 9/4	38.0	22.6	R
9/5	1400	I (F-I)	2BB	3.0	ALT 8/8†	21.6	12.2	R

* RR, strong repulsion; R, weak repulsion; O, no apparent response except sensing; A, weak attraction; AA, strong attraction.

† Sweat collected by sponge.

TABLE 9

RESPONSE OF NORMAL BLACKTIP SHARKS (NB), BLINDED BLACKTIP SHARKS (BB), AND NORMAL SHARKS (NG) TO HUMAN SWEAT AT ENIWETOK LABORATORY, 1960

DATE (1960)	TIME	TANK	SHARKS	SWEAT (ML)	DONOR, DATE	ACTIVITY INDEX		RESPONSE*
						Controls	Test	
6/30	1250	I (A-D)	2NG	3.0	ALT 6/29	14.6	13.2	R
	1340	I (A-D)	2NG	3.0	ALT 6/29	12.2	8.0	R
	1350	I (A-D)	2NG	5.0	ALT 6/30	—	7.4	R
	1530	I (A-D)	2NG	3.0	ALT 6/29	13.8	10.0	R
	1555	I (A-D)	2NG	6.0	ALT 6/29	8.7	8.6	O
7/1	1007	I (A-D)	2NG	3.0	ALT 6/29	17.0	18.0	O
	1035	I (A-D)	2NG	6.0	ALT 6/29	17.8	17.6	O
	1105	I (F-J)	2NG	3.0	ALT 7/1	13.2	7.0	R
	1130	I (F-J)	2NG	6.0	ALT 7/1	7.4	8.3	O
	1400	I (A-D)	2NG	6.0	ALT 7/1	13.6	8.8	R
	1422	I (F-I)	2NG	6.0	ALT 7/1	14.0	12.2	R
	1942	I (A-D)	2NG	6.0	ALT 7/1	22.4	17.8	R
7/2	0903	I (A-D)	2NG	6.0	ALT 7/1	18.4	18.6	O
	1140	I (F-I)	2NB	3.0	ALT 7/2	50.5	92.8	A?
	1430	I (F-I)	2NB	6.0	ALT 7/2	68.5	71.1	O
	1445	I (A-D)	2NG	9.0	ALT 7/2	18.4	15.6	R
7/6	1300	I (A-D)	2NB	5.0	SK-ALT 7/2	52.2	23.2	RR
	1400	I (F-I)	2BB	6.0	JK 7/6	31.4	31.0	R?
	1430	I (A-D)	2NB	6.0	SK 7/6	47.0	31.4	R
7/7	0905	I (A-D)	2NB	6.0	JK 7/6	40.8	33.8	R?
7/9	1010	I (A-D)	2NB	3.0	SK 7/6	20.0	7.0	RR
	1500	I (A-D)	2NB	3.0	JK 7/6	22.6	5.4	RR
7/11	0839	I (A-D)	2NB	3.0	SK 7/6	33.0	29.0	R
	1549	I (A-D)	2NB	3.0	JK 7/6	31.4	10.4	RR
7/19	1055	I (F-I)	2BB	3.0	SK 7/6	24.6	14.2	RR
	1120	I (A-D)	2NB	3.0	SK 7/6	31.4	31.6	R?
	1145	II (A-C)	2NG	3.0	SK 7/6	7.8	10.0	O
7/20	1505	I (F-I)	4BB	3.0	JK 7/6	25.4	18.6	RR
	1530	I (A-D)	4NB	3.0	JK 7/6	15.4	15.2	R
7/23	1243	I (F-I)	4BB	3.0	SK 7/11	20.4	24.8	O
7/24	1450	I (F-I)	4BB	3.0	ALT 7/23	23.8	22.6	R
	1655	I (A-D)	4NB	3.0	ALT 7/23	28.8	13.2	RR
7/25	0940	I (F-I)	4BB	3.0	ALT 7/23	25.2	18.4	R
	1020	I (A-D)	4NB	3.0	ALT 7/23	33.8	25.4	R
8/25	1230	I (F-I)	4BB	3.0	ALT 8/25	28.0	26.2	R
	1300	I (A-D)	4NB	3.0	ALT 8/25	34.0	32.2	R

* RR, strong repulsion; R, weak repulsion; O, no apparent response except sensing; A, weak attraction; AA, strong attraction.

periments were conducted at the Hawaii laboratory on the population of sharks in Pond 5, which at that time consisted of a tiger, a hammerhead, and a grey shark. The method of "point introduction" was used. During tests, three or four uninjured fish (*Tilapia mosam-*

bique) were confined in the 5-gal funnel of sea water on top of the tower. During tests, the water from the funnel containing the fish was introduced through the hose. This produced a strong hunting response in the hammerhead. The response of the tiger shark and the grey

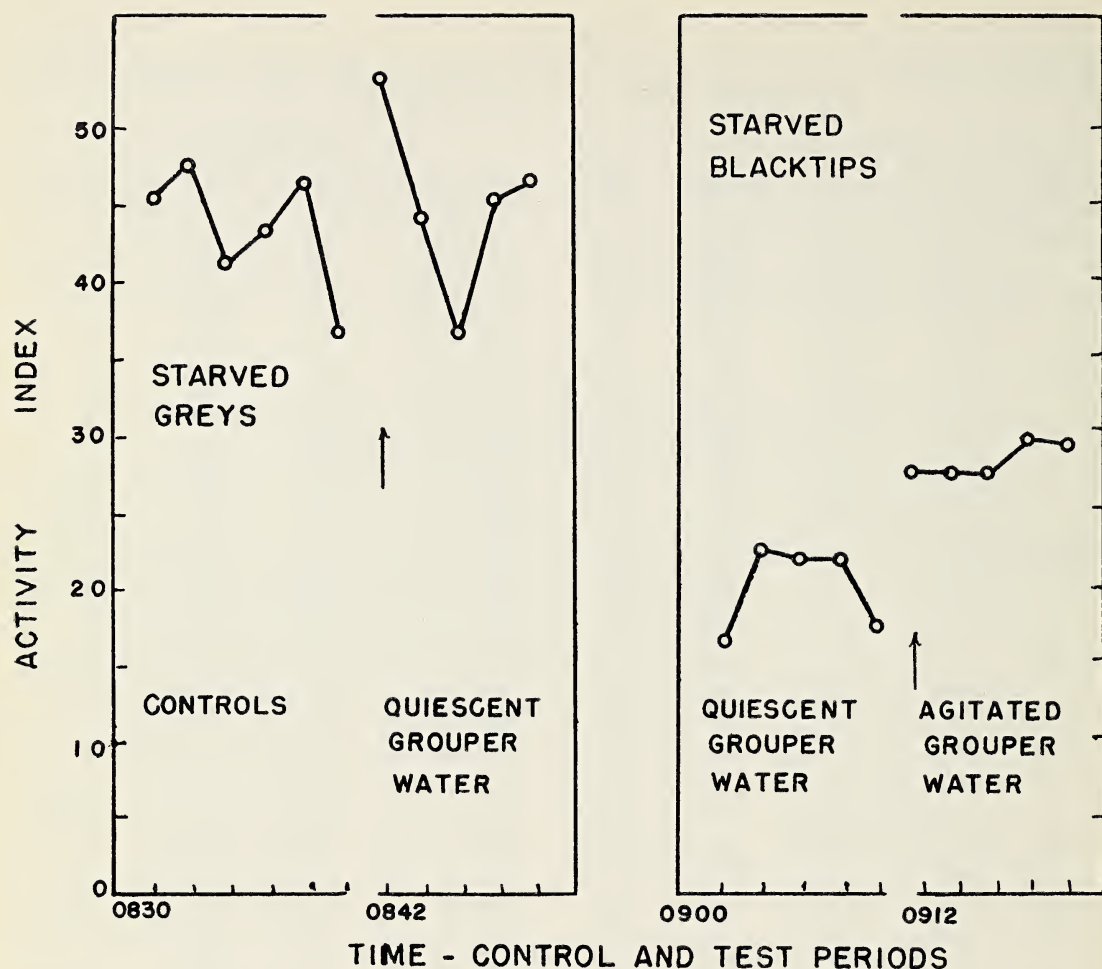


FIG. 10. Activity index during successive 2-min periods, illustrating response of starved grey sharks to "quiescent grouper water" and of starved blacktip sharks to "agitated grouper water."

shark was positive but less intense. "Tilapia water" was the attractant used in the experiment involving human sweat which was described earlier.

Several, more definitive experiments were conducted at Eniwetok during the summer of 1960 using an experimental arrangement illustrated in Figure 9. Living fish were placed in a 25-gal plastic container into which sea water was flowing. The sea water could be siphoned from the container into the test area of either Tank 1 or Tank 2, or it could be spilled to the ground. The compartment of Tank 1 contained four starved blacktip sharks and that of Tank 2 held four starved grey sharks, all with normal

vision. One observer, manipulating the siphons and living "prey" fish, was concealed from the sharks by a blind; a second observer, recording data on shark behavior, was concealed in the observation booth.

Only two of several experiments will be described in detail. In one (Fig. 10), four groupers (*Epinephelus merra*) had been placed in the container the previous night, with the water siphoning into the blacktip compartment. In the morning, following a series of control periods which started at 0830 (timed on a 24-hr clock), the "quiescent grouper water" was siphoned into the grey shark compartment. In the first test period (at 0842) the grey sharks

showed obvious awareness and mild attraction, with one shark biting the siphon tube, but the response quickly subsided. Siphoning into the blacktip compartment was then resumed (at 0900) with no noticeable response from the sharks; this was anticipated as the water had been siphoning into this compartment all night. The groupers were then frightened and excited by threatening them with a moving stick. There followed a noticeable hunting reaction by the blacktips (at 0912), stimulated by the "agitated" grouper water. Similar results were obtained with both starved blacktip and grey sharks using quiescent and agitated surgeon fish and mullet in place of the groupers.

In the second experiment to be described in detail (Fig. 11), the grey sharks showed a normal behavior pattern during control periods which started at 1600. When "quiescent grouper water" was introduced (at 1612) they responded,

as above, with a mild hunting reaction; one bit the tube and others milled near it. In the meantime, a small grouper had been removed from the aquarium and held in a dip net in air for 30 min, at which time it was still alive and apparently undamaged. With the water from the quiescent groupers still flowing into the grey shark compartment, the "distressed" grouper was quietly lowered into the container (at 1622) by a string tied around its body; it was removed after the third test period (1628). The sharks displayed a violent hunting reaction with circling and biting of the tube. The "quiescent grouper water" continued to siphon into the compartment for about 1 hr, at which time (1730) the sharks exhibited normal activity during control conditions. The small grouper which had been returned to the dip net and was still alive after 74 min, was again lowered into the container (at 1740) for three test periods.

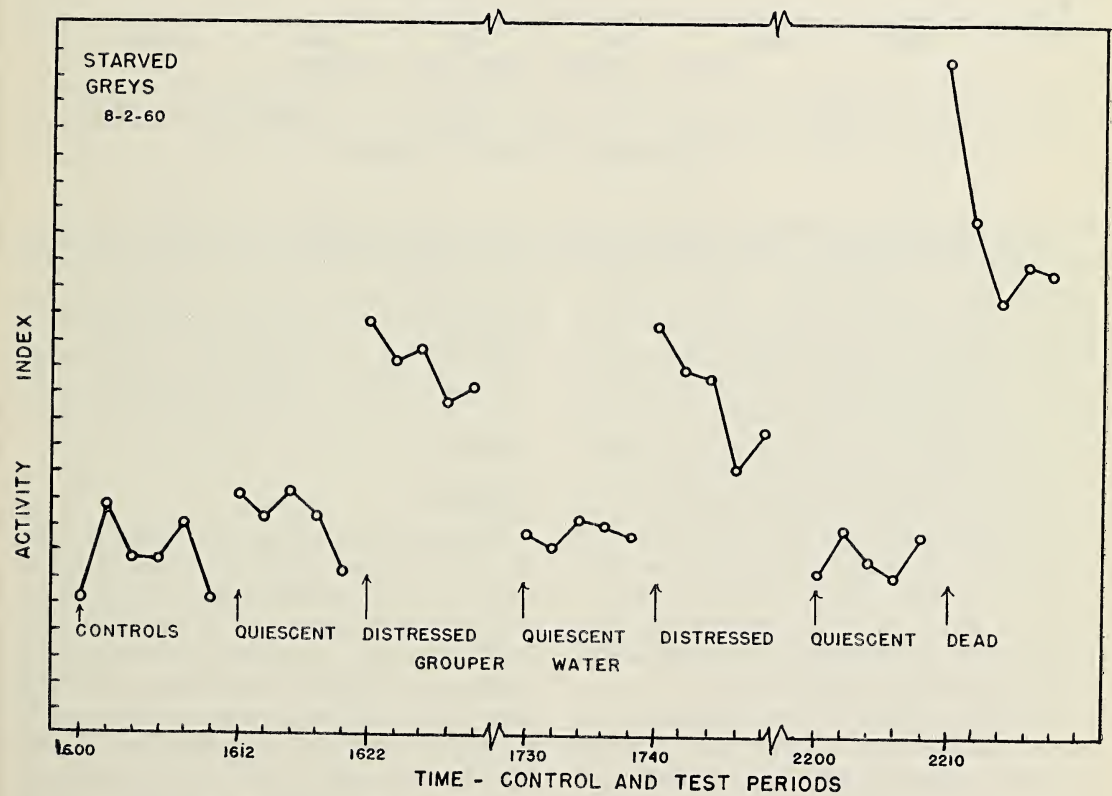


FIG. 11. Activity index during successive 2-min periods, illustrating response of starved grey sharks to "quiescent grouper water," to "distressed grouper water," and to "dead grouper water."

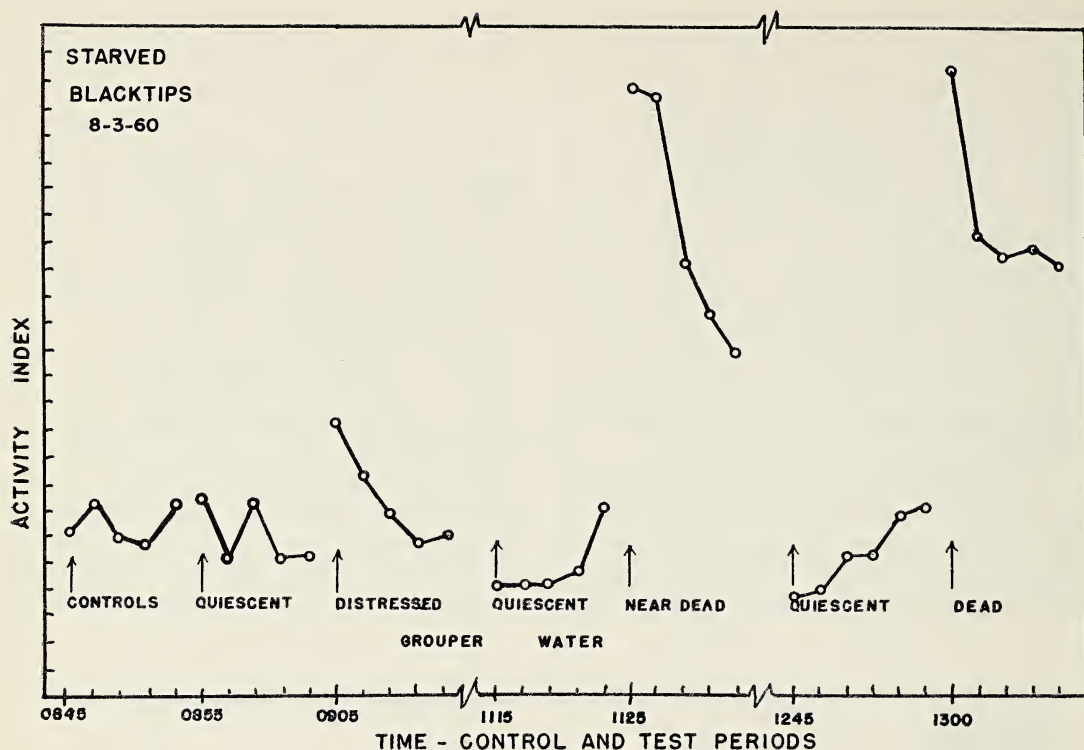


FIG. 12. Activity index during successive 2-min periods, illustrating response of starved blacktip sharks to "quiescent grouper water," to "distressed grouper water," and to "dead grouper water."

The sharks again responded with a violent hunting response and tube biting. The procedure was repeated after an additional 4 hrs (at 2200) during which time the quiescent grouper water had been flowing into the compartment and the sharks were responding normally. The small grouper in the dip net, however, had died. After the dead fish was lowered into the container (at 2210), there was a spectacular hunting reaction by the sharks. Only the string was recovered from the container at the end of the third period: the small dead grouper had been swallowed by one of the larger "quiescent" groupers. The water in the container was clear indicating that the fish had been engulfed whole without the escape of body juices.

The above experiment was repeated on the starved blacktip sharks, using the same four "quiescent" groupers and another "distressed" grouper. In this case the "distressed" grouper was not eaten after it had died. The results (Fig. 12) were almost identical to those obtained with

the starved grey sharks. A similar test using four "quiescent" and one "distressed" mullet gave similar results (Fig. 13). The sharks even responded to a small "distressed" blacktip shark which was held in a dip net for a few minutes and then, still alive, was lowered into the container, in this case in the absence of any "quiescent" fish.

Discussion

These experiments show that "quiescent" prey give off an odor which can be detected by sharks when it is first introduced into their environment but to which they soon become habituated. There is still the question, of course, as to whether the "quiescent" fish were still under stress because of the artificial environment of the plastic container. Regardless of this, the experiments demonstrate that when the prey becomes frightened and excited it gives off an additional or a new odor which again stimulates the habituated sharks, provoking the typical

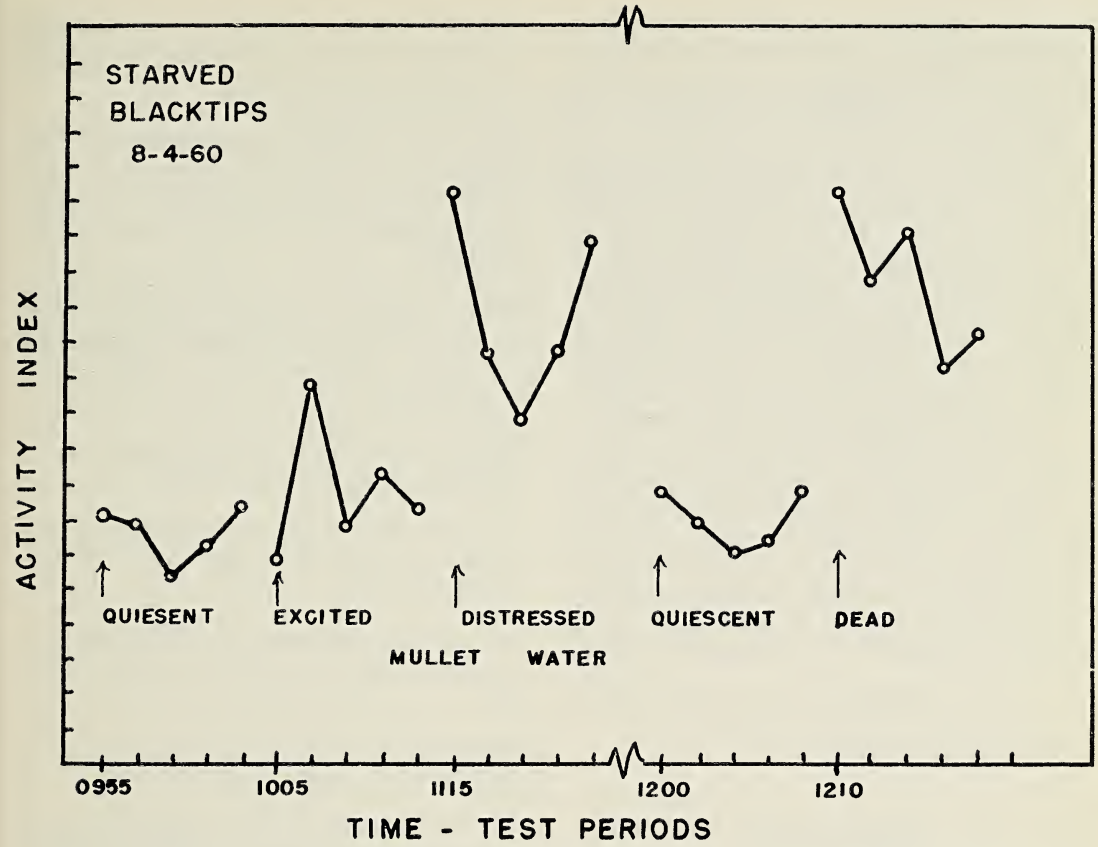


FIG. 13. Activity index during successive 2-min periods, illustrating response of starved blacktip sharks to "quiescent mullet water," "excited mullet water," "distressed mullet water," and "dead mullet water."

hunting response. Moreover it seems that shark activity, and thus presumably the amount of odorous material released, increases with increased agitation of the prey.

It seems unlikely that the odorous material is associated with body juices released by direct injury to the prey on the part of the observer. The fish used were healthy aquarium specimens which in some cases, e.g., groupers, were used over and over again and yet suffered no obvious ill-effects from being repeatedly "agitated." It is unlikely they would be damaged by rubbing against the sides of the smooth plastic container. They could, of course, rub against each other when excited. This may possibly have removed part of their mucous coating and enabled body juices to escape through the skin.

That the results were not induced by the artificial environment of the shark tanks was dem-

onstrated in follow-up experiments with sharks in the natural environment of Eniwetok lagoon by Hobson (1963). Water siphoned into the lagoon from a plastic container in which large, living, agitated but apparently undamaged groupers had been placed, attracted both white-tip (*Triacodon obesus*) and grey (*C. menisorah*) sharks. They detected the "grouper water" from a distance and followed its path upstream to the source—a concealed plastic tube.

If the substance which attracts the sharks is released by some subtle damage to the skin of the prey it might be similar to that demonstrated by von Frisch (1941) in the injured skin of the minnow (*Phoxinus laevis*). As with von Frisch's material, identified as a purine- or pterin-like substance by Hüttel (1941), it might produce an alarm reaction among the prey but still be attractive to the sharks. On the other

hand it is tempting to postulate that the substance is some metabolite which is released from gill, vent, or skin by excitement rather than by injury of the prey.

Whatever may be the source and nature of the attractant, we have presented evidence that olfaction is involved in the predation of sharks on normal, healthy fish. It is suggested that in the natural environment, fish give off odors to which the sharks are conditioned. It is further suggested that when the fish become frightened or excited, and certainly if they rub against each other or against a coral head, they give off additional or new odors which stimulate the hunting response in sharks. This hypothesis is consistent not only with our experimental data but also with our observations of the behavior of the sharks in their natural environment. For the most part they display a complete disregard for the myriad of normal, healthy fish which surround them. However they are able to track down and converge on a distressed fish (such as a live fish suspended from a hook through the jawbone but otherwise uninjured) with uncanny speed and accuracy.

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Feeding Behavior in Three Species of Sharks¹

EDMUND S. HOBSON²

THIS REPORT concerns a study of the feeding behavior in three species of sharks: *Carcharhinus menisorrhah* Müller and Henle, the grey shark (Fig. 1), *Carcharhinus melanopterus* Quoy and Gaimard, the blacktip shark (Fig. 2), both of the family Carcharhinidae; and *Triaenodon obesus* Rüppell, the whitetip shark (Fig. 3), of the family Triakidae. The study was conducted in the lagoon at Eniwetok Atoll, Marshall Islands, during the summers of 1959 and 1960. It was a segment of a broad program of investigation of shark behavior in which laboratory and field work were coordinated whenever possible. The overall program, conducted at both the Eniwetok Marine Biological Laboratory and the Hawaii Marine Laboratory, Coconut Island, Hawaii, was under the direction of Dr. Albert L. Tester, with financial support from the Office of Naval Research (Contract Nonr 2756(00), Project NR 104503).

Observations of sharks in their natural environment have been the basis for most of the shark literature which is available today and yet comparatively little has been offered toward a realistic understanding of shark behavior. Most of this material has been written for popular consumption and is therefore oriented toward the sensational rather than the scientific.

We do find scientifically oriented accounts in the literature (as for example, Eibl-Eibesfeldt and Hass, 1959; Limbaugh, 1958; and Wright, 1948) but these observations are limited largely to incidental encounters.

A critical study of shark behavior, undertaken with planned experiments in the sharks' natural

environment—the aim of this investigation—has been almost completely neglected.

In this study, a comparison is made of the feeding behavior of the three species. Behavior is further related to habitat and to distribution within the lagoon. Experiments designed to illustrate the roles played by the major sensory modalities are presented. This last portion of the investigation, dealing primarily with grey sharks, includes a consideration of the specific stimuli involved in releasing feeding behavior. Consideration is also given to food preferences and to factors which may possibly inhibit feeding.

GENERAL DESCRIPTION OF STUDY AREAS

The study was centered about two primary locations: (1) the lee of Engebi Island during 1959, and (2) the lee of Bogen Island, adjacent to Deep Channel, during 1960. The Engebi Island site was in 15 ft of water over a relatively shallow sand and coral rubble flat extending out from shore for approximately 400 yd before dropping suddenly into the deeper regions of the lagoon. Currents are weak in this area and the water is generally turbid, with underwater visibility commonly less than 20 ft. At the Bogen Island site strong tidal currents are present and underwater visibility often exceeds 100 ft. The edge of Deep Channel at this point drops abruptly from a depth of approximately 10 ft at the rim to 110 ft at the bottom.

At these locations, observations were made from the following vantage points:

1. An underwater chamber was fitted to a vessel moored in the lagoon. This chamber was a metal cylinder, 14 ft long and 2½ ft in diameter, open at the top and closed at the bottom, with viewing ports on three sides near the bottom. An observer in the chamber was situated approximately 8 ft below the surface.

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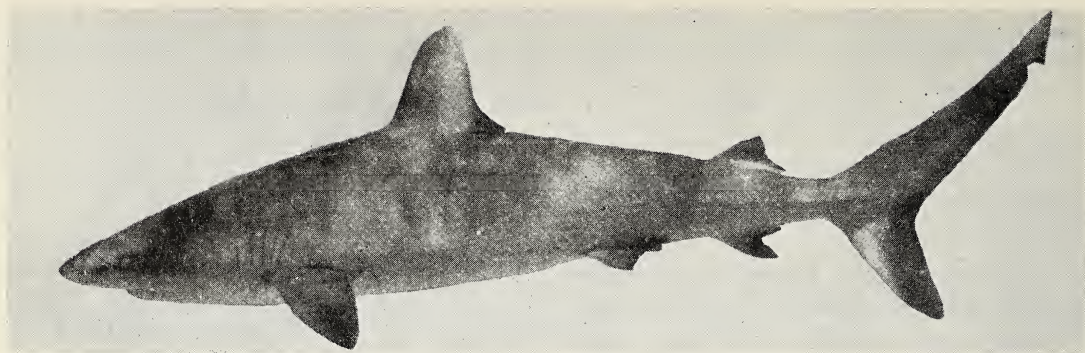


FIG. 1. The grey shark, *Carcharhinus menisorrhah*. (Photo by E. Hobson.)

2. A wire cage was suspended from a raft anchored on the slope at the edge of Deep Channel. An observer in this cage was located immediately below the surface.

3. A canvas screen, anchored on the bottom, concealed an observer lying prone on the bottom wearing SCUBA equipment.

4. A 16-ft glass-bottom boat, having the added advantage of mobility, provided for observations of activity directly below.

5. In many cases, the observations involved incidental encounters with sharks during the course of such routine underwater activity as installing apparatus, etc.

Experimental procedures and apparatus will be further described as they pertain to the report.

SPECIES STUDIED

Identification of the sharks is based on Schultz et al (1953). All three species, *Carcharhinus menisorrhah*, *C. melanopterus*, and *Triaenodon obesus*, reportedly have a wide Indo-Pacific distribution. They are reported from the Red Sea as well as the Maldive Islands by Klausewitz (1958, 1959). Although positive identification of the two carcharinids awaits a revision of the family on a world-wide basis, all three species appear to be prominent in the shark populations of most Pacific atolls. Harry (1953) reports them from the Tuamotus, as does Randall (1955) from the Gilbert group. The author found them abundant at Palmyra and they were the only species of sharks consistently seen in the lagoon at Eniwetok during the present investigation.

GENERAL OBSERVATIONS OF BEHAVIOR

Often when we were engaged in various types of activity in the lagoon the resulting commotion, which commonly involved splashing on the surface or striking metal tools on hard objects underwater, was immediately followed by the rapid approach of an obviously alerted blacktip or grey shark.

In spite of this initial attraction to many stimuli, both species exhibited varying degrees of caution when encountering unfamiliar situations. This was particularly apparent in the blacktip, a species which seemed especially sensitive to potential danger. When work was begun at Engebi, blacktips often circled at the limit of visibility in the baited area for as long as 2 or 3 hr before approaching the bait. Then, when an approach was made, it seemed to be done reluctantly and was often cut short by some stimulus, unnoted by the observer, which startled the shark as it neared the bait and caused it to swim rapidly away. Usually the shark repeated the approach, but in these early tests it was not until several sharks had become active in the area that a blacktip finally took the bait. We subsequently found that we were dealing with the same blacktips day after day at Engebi and that as the work progressed, their initial caution steadily declined. This was presumably due to a growing familiarity with the situation. Nevertheless, a month of testing passed before the blacktips took the bait without hesitation. Once released, the attack of the blacktip was very fast and aggressive.

The grey was a notably bolder species. Al-

though a blacktip often approached rapidly in response to splashing at the surface, it then generally reversed direction and retreated just as rapidly if the investigation of the splashing brought it into an encounter with a human. In the same situation, the grey ordinarily reacted to the encounter with a human by continuing the approach to approximately 5 yd from the human, at which point it would veer aside and circle with an apparent cautious interest. If no further stimuli were introduced, the grey moved on.

Blacktips and greys showed a marked increase in excitement when feeding in numbers. This phenomenon, generally referred to in extreme cases as the feeding frenzy, has been observed in many species of sharks. In the blacktips and greys, the presence of more than one shark appeared to lower the threshold for the release of feeding behavior.

Whitetips did not show this group effect. Even when feeding in numbers, members of this species responded individually and without a notable increase in excitement. The whitetip seemed to be relatively unresponsive to many of the stimulus situations which elicited a sharp reaction in the grey and blacktip. There was little overt response seen in this shark when encountering a human in the water for the first time. In this situation we did not see the curiosity frequently exhibited by the greys, nor the start and rapid flight usually exhibited by the blacktip.

On several occasions whitetips appeared and

took fish from the spears of divers before the fish could be removed from the water. Even in these instances, the slow, deliberate actions of this shark did not give the impression of being a threat to the diver. This impression may have been an illusion based on the sluggish behavior of the animal. On one such occasion a 6-ft whitetip bit the fish in half and then made a slow pass at the diver holding the other end of the spear. This appeared to be a warning pass at a potential competitor rather than an active attack. Such warning passes were noted on several occasions directed at grouper or snappers which approached a bait that was under attack by a whitetip. Similar behavior was noted in greys and blacktips. Tester (personal communication) observed a small blacktip pursue a grouper of comparable size from a bait which had been placed on the bottom in shallow water near Aniyaani Island. In this case, the blacktip showed considerably more than a warning pass as it actively pursued the grouper among a concentration of small coral heads. We did not observe these sharks exhibiting aggressive behavior toward members of their own species. One observation made on numerous occasions might at first glance seem to oppose this view. When a bait which was too large to be immediately swallowed was presented to a group of feeding greys or blacktips, the shark which succeeded in taking the bait would invariably swim rapidly away from the area, shaking its head vigorously from side to side presumably in attempts at cutting up and swallowing the bait. As it fled,

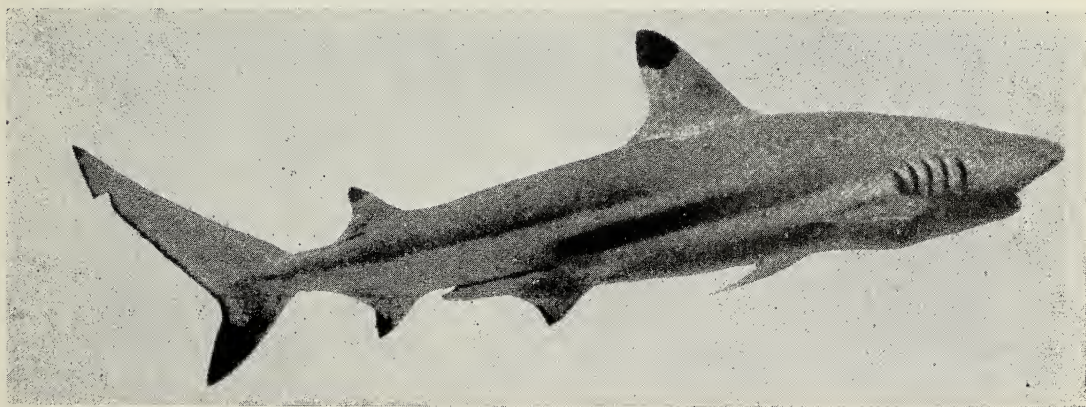


FIG. 2. The blacktip shark, *Carcharhinus melanopterus*. (Photo by E. Hobson.)

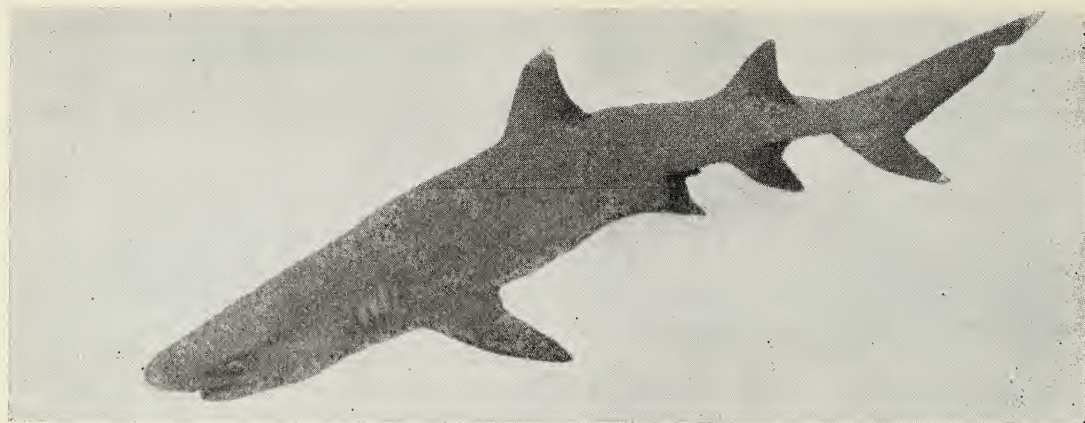


FIG. 3. The whitetip shark, *Triaenodon obesus*. (Photo by E. Hobson.)

the other sharks always followed in close pursuit. Although the flight of prey was commonly noted to release attack in the grey, the aggressive behavior of these other sharks in this case was believed to have been directed against the bait rather than the fleeing shark.

There was never any mistaking an alerted grey or blacktip from one engaged in normal patrolling activity. Thus we had no difficulty distinguishing a grey or blacktip entering the test area in response to a stimulus situation we had presented from one incidentally passing through the area. The movements of the alerted greys and blacktips were markedly accelerated and the grey in particular seemed tense and highly responsive to subsequent stimulation. Movements of the grey immediately before attack were markedly abrupt; its body often appeared stiff, with back slightly arched and head extending straight out and slightly upward. The pectoral fins were characteristically pointed noticeably downward. Attack was prefaced in many cases by such anticipatory movements as a lateral shaking of the head (noted also by Eibl-Eibesfeldt and Hass, 1959) and a movement of the jaws as in biting (Hobson et al., 1961).

Although it was not always so easy to make this distinction with the seemingly unresponsive whitetip, these sharks were undoubtedly more responsive than they appeared to be. It is likely that their reactions were simply more subtle than those of the more excitable greys and blacktips. Whitetips usually appeared in

an area shortly after divers had undertaken various types of underwater activity. However, after their appearance the whitetips would swim about without any apparent interest in the proceedings. Nevertheless, the consistency of these appearances indicated that the sharks sensed activity and were interested.

DISTRIBUTION OF SPECIES WITHIN LAGOON

Blacktips were the most commonly observed shark over the sand and coral rubble flats lying under approximately 1–40 ft of water at the perimeter of the lagoon. These flats extend out from shore for distances ranging from approximately 50 yd to several miles before the bottom falls off sharply into the depths. Coral growth in this area is generally restricted to large isolated heads which, in many cases, reach the surface of the water at low tide. Although blacktips exceeding 6 ft in length were seen, specimens of more than 4 ft were not common. Small blacktips were very common on the seaward reef flats when the sea covered these flats at high tide. The seaward flats were largely exposed at low tide.

The whitetip also frequented the shallow waters of the lagoon, although unlike the blacktip, which foraged widely over the flats, the whitetip centered its activity among the coral heads and about the coral-rock ledges which border the seaward passages. Unlike the other two species, the whitetip was commonly seen resting motionless on the bottom, often under

ledges and in caves. The whitetip was common to a length of 6 ft, with individuals of 7 ft seen on occasion.

We seldom encountered the blacktip when we moved down the slopes from the shallow flats into the deeper waters of the lagoon or seaward passages, but here we found the grey shark in abundance. A census of the shark popu-

lation of the entire lagoon would probably show the grey shark to be the most numerous. This shark was commonly seen up to 7 ft in length.

All three species were generally observed swimming close to the bottom unless drawn toward the surface to feed.

Figure 5 shows shark sightings by species during a period of 30 days in the vicinity of



FIG. 4. The test area off Bogen Island, showing the relative position of Deep Channel (top), raft (at edge of channel), and the barge. The island is out of the picture to the left. (Photo by R. A. Boolootian.)

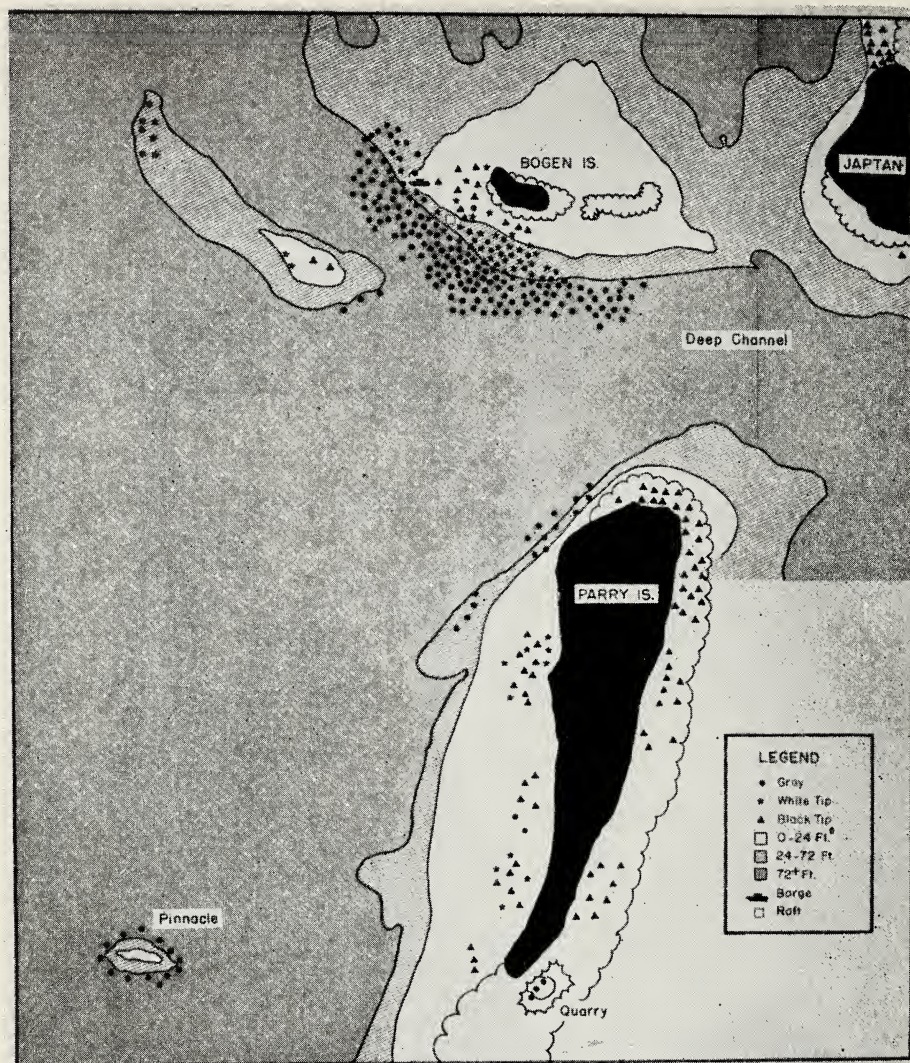


FIG. 5. Area in the vicinity of Parry Island, showing the sharks sighted during the period 26 July to 26 August, 1960, and indicating species involved and depth of water where sighting occurred.

Parry Island and the depth of water in which these sightings occurred. Two basic rules were observed in making this count: (1) no more than one count was made in any one area on any one day; (2) if there was any question of whether or not a particular shark had already been counted on any one day, then this shark was disregarded. This survey was not intended to show shark abundance, but rather to illustrate the areas and depths in which each of the three species was normally seen.

The distributional picture which emerges is consistent with the observations made throughout the program. For example, during 2 months of work in 15 ft of water off Engebí, only two grey sharks, both approximately 2 ft in length, were seen. On the other hand, the experiments involved many blacktips and whitetips. In contrast, when experiments were conducted along the edge of the dropoff into Deep Channel, both whitetips and greys were in abundance, while blacktips were only occasionally seen.

In December 1959, while fishing outside the seaward reef slope at Palmyra, we saw only grey sharks, finding these in considerable abundance. At the same time, only blacktips were common on the reef flat a hundred yards away. We saw comparatively few whitetips at Palmyra, these in shallow water over the reef. Klauswitz (1959) found these same species occupying similar habitats in the Red Sea.

Exceptions to this general distribution pattern were noted. Large grey sharks appeared at poison stations in water scarcely 6 ft deep, while whitetips were seen swimming over open bottom, far from the nearest coral head or rock. Furthermore, Strasburg (1958) reports the catching of two blacktips at sea in the Marquesas.

BEHAVIOR AND HABITAT

The sluggish behavior noted in the whitetip is consistent with a life in and about the caverns and crevices of the coral reef. This species was noted as being clumsy and ineffective in attempts at taking baits which were suspended in midwater. However, this same shark was remarkably effective in tracking down and capturing prey which had taken shelter deep in one of the many holes or crevices typical of a coral reef, thus making available to it prey which are beyond the reach of both greys and blacktips. Considerable time was spent placing wounded fish far back into small holes in the reef and then watching as a whitetip appeared, nosed about tentatively for the correct hole, and then swam in and captured its prey. Large whitetips were seen disappearing into small holes from which they presently emerged, always head first. The experiment described below involved whitetips and greys and illustrates the division of the food source between these two species.

Experiment 1

Three small wounded fish, each essentially identical, were presented simultaneously at three positions below the raft at the edge of Deep Channel, where water depth was approximately 35 ft: (1) Suspended mid-way between surface and bottom; (2) on the bottom in an exposed position; (3) concealed in a hole beneath a large rock on the bottom.

Bait 2 was lowered to the bottom at the end of a weighted line. Baits 1 and 3 were both secured to a single line which ran from the raft, down under one side of the rock, through the hole, out the other side and back up to the raft. By alternately hauling in one end of the line or the other, both baits could be simultaneously hauled aboard the raft or lowered into position.

The experiment was repeated 16 times when both greys and whitetips were in the vicinity. Although the two species seemed equally adept at taking the exposed bait on the bottom, the suspended bait in all but one instance was taken by a grey, while the whitetips completely monopolized the bait concealed in the hole.

When grey sharks encountered humans in shallow water they often started and fled in much the same manner described for the blacktip, rather than exhibiting their usual relatively bold inquisitive approach. Possibly this apparent change in behavior was a result of their being out of their usual habitat. This observation might offer an insight into the characteristically timid behavior of the blacktip. Perhaps this apparent timidity is an adaption of these relatively large animals, which must remain in motion, to a shallow water habitat. The shark, unable to take shelter and without room to maneuver, may find flight the alternative. In the blacktips, this characteristic timidity is more apparent in the larger individuals. The suggestion that this behavior might have some survival value implies the existence of a natural predator. The only evidence we found of such a predator was the presence of an 18-inch blacktip in the stomach of an 80-lb grouper.

DETECTION AND CAPTURE OF FOOD

Sharks are well known to feed avidly on dead fish, meat, and many other food materials dumped as garbage or used as bait. It is also well known that they will consume living fish impaled on a hook or spear. These, however, are unnatural situations. Undoubtedly, under natural conditions these sharks will feed on such prey as may have been killed or weakened by disease or injury. The sharks in the Eniwetok lagoon, as elsewhere, are highly responsive to stimulus situations which suggest injured and/or distressed, as well as dead or moribund

prey. Nevertheless, it seems unlikely that this source of food alone is sufficient to support such a large shark population. It seems probable, then, that they act not only as opportunistic scavengers, but also as predators on healthy free-moving animals. Eibl-Eibesfeldt and Hass (1959) report observing both *C. menisorrh* and *C. melanopterus* in the Indian Ocean herding schools of mullet against the shoreline and actively feeding on these fishes. Similarly, Strasburg (1958) observed pelagic whitetips (*Pterolamiops longimanus*) herding squid under a night light. Strasburg also cites other evidence of pelagic sharks apparently capturing what would appear to be highly motile elusive prey.

We observed no such activity among the three species in the lagoon at Eniwetok. These sharks seemed oblivious to the presence of the numerous reef fishes which were continually present during the shark's patrolling activities. This behavior might be expected, however, as only under such conditions would the reef fishes allow sharks to move in amongst them without exhibiting immediate alarm and taking shelter. This same apparent oblivion to what appears to be potential prey is also standard behavior seen in many other reef predators, for example the groupers, snappers, and moray eels. It seems likely that this behavior on the part of the predators is advantageous in allowing them to catch their prey unawares with a frequency which, while sufficient to maintain life, does not destroy the illusion of their non-aggressiveness. It is also probable that the threshold for the release of feeding on healthy prey fluctuates with the relative availability of more readily obtainable food items, such as dead or disabled fish.

The present study is confined to feeding behavior with respect to dead, damaged, and distressed prey. An effort is made to determine which of several sensory modalities are involved and which are dominant in the sequence of events between initial stimulation and the act of consuming the prey.

RESPONSE TO OLFACTORY STIMULI

A number of experiments were conducted which elucidated the role of olfaction in detect-

ing dead and living prey. Only three (II, III, and IV) will be reported in detail.

Experiment II

This experiment was designed to study the response of these sharks to an uninjured fish struggling on a line, which might thus produce visual, mechanical, auditory, and perhaps olfactory cues.

The glass-bottom boat was anchored in 40 ft of water on the steep slope of Deep Channel where the current ran in one of two directions, depending on the tide. Ten trials were conducted, each at a time of strong flood or ebb current when visibility was good. As a precaution against the sharks becoming conditioned to feeding at this location, the trials were spaced over a period of several weeks, with only one trial on any one day. Each trial involved one fish, either a grouper (Serranidae), snapper (Lutjanidae), or mullet (Mugillidae), 2 to 3 lb in weight, secured to a line by a piece of soft, light cord which passed through the membrane behind the maxillary. The fish had been caught by barbless hook and kept in tanks at the laboratory until needed; they appeared to be healthy and uninjured.

Before the fish was lowered to a point 5-10 ft above the bottom, a 5-min observation period was conducted to insure that no sharks were in the area. If sharks were seen the test was delayed until at least 5 min after they had disappeared.

Observations included species of shark, the time each took to locate and take the bait, its general behavior, and particularly the nature and direction of its approach. It was presumed that if the sharks approached directly and consistently from downstream the attracting stimulus had been initially olfactory, inasmuch as only the olfactory stimulus was affected by the current. If the approach was from random directions, then other sensory cues, such as visual, were likely to be involved in the initial attraction.

The results are summarized in Table 1. In 9 of the 10 trials the sharks appeared from downstream, swimming rapidly and directly toward the bait, thus indicating they were responding to olfactory cues carried by the current. The

TABLE 1
RESPONSE OF SHARKS TO FISH WHICH ARE STRUGGLING ON A LINE (EXPERIMENT II)

TRIAL	BAIT	TIDAL CURRENT	NO. AND LENGTH OF SHARKS INVOLVED	TIME TO APPEAR	DIRECTION FROM
1	mullet	flood, moderate	1 4-ft grey	17 min	downstream
2	mullet	flood, strong	1 4-ft grey	10 min	downstream
3	grouper	flood, moderate	2 6-ft greys	15 min	downstream
4	snapper	flood, moderate	2 4-ft greys	20 min	downstream
5	grouper	flood, moderate	1 6-ft grey	18 min	downstream
6	mullet	flood, moderate	1 4-ft grey	5 min	downstream
			1 6-ft grey		
7	mullet	ebb, moderate	2 4-ft greys	10 min	downstream
8	grouper	flood, moderate	1 4-ft grey	16 min	downstream
			1 3-ft whitetip		
9	grouper	ebb, moderate	2 6-ft greys	14 min	downstream
			1 6-ft whitetip		
10	grouper	ebb, moderate	2 4-ft greys	25 min	upstream

one test which might at first glance appear to deviate from this pattern deserves quotation from the field notebook:

Introduction was made at 1035 . . . bait positioned 10 ft off the bottom, being carried 20-30 yd astern by the current where it struggled vigorously until 1050 when noticeably tired. By 1055 bait no longer struggled, but simply maintained position, looking quite natural. At 1100, two 4-ft grey sharks appeared from upstream, cruising slowly along the bottom toward the test area and giving no indication of having sensed bait. When still about 20 yd upstream of the boat (and 40 ft down, on the bottom) they both became noticeably alerted. At this point apparently they had become aware of the boat on the surface, as they veered upward and swam at an accelerated rate directly to within 5 yd of the boat, turned aside at this distance and circled twice. Then, seeming to lose interest, they returned slowly to the bottom and continued at their leisurely pace downstream, passing within 10 yd of the bait without apparent notice (as stated, the bait was not struggling, but merely maintaining position in the current). The sharks continued downstream approximately 20 yd below the bait, at which point they both obviously and simultaneously became alerted, turned around, and with increasing speed raced back upstream straight toward the bait, with one of them taking it.

The first response in the above observation was apparently one of vision to the boat on the surface. The second response, in which the sharks returned upstream to the bait, was obviously one of olfaction.

In this experiment, the sharks appeared to be following an olfactory cue in a direct line to an uninjured fish. However, there was no as-

surance that other stimuli were not also involved in the detection and approach to the bait. The question arises whether these sharks can follow an olfactory cue directly to its source in the absence of other cues.

The classical experiments of Parker (1914), in which he observed the approach of dogfish to bait when both nostrils were free and when one was occluded, has been offered as proof that directional response to olfactory cues is possible by virtue of the ability of each nostril to detect minute differences in the concentration of odoriferous material. In standing water in the ponds at Coconut Island we have observed the hammerhead (*Sphyrna lewini*) describing the typical figure 8 pattern, described by Parker, in which the shark is apparently locating the source of stimulation by continually turning toward the nostril exposed to the greater concentration of the material. Tester (1963) also describes how blinded blacktips spiral down from above in converging on bait on the floor of the tanks at the Eniwetok Marine Biological Laboratory. It seems likely that sharks are capable of following an olfactory trail in running water, particularly when the current is strong and the trail narrow, thus forming what would essentially be an olfactory corridor. Under such conditions they could be expected to make a direct-line approach by taking advantage of the normal lateral movements of the head, which are part of the swimming motion, in keeping themselves oriented in the stimulus trail.

Experiment III

The purpose of this experiment was to determine if these sharks are capable of orienting themselves in a current and following an olfactory corridor in a direct line to its source in the absence of other stimuli.

A location on the edge of Deep Channel similar to that used in Experiment II was chosen. Essentially clear, colorless fish extracts were used as the olfactory cues. These were prepared from several species of grouper but always of the same concentration (600 gm of fish flesh or skin macerated in a Waring blender with 6 liters of fresh water and diluted in a large plastic container with 64 liters of sea water). The material was introduced from the glass-bottom boat by siphoning from the container through a clear plastic $\frac{3}{4}$ -inch hose which ran down to the top of the reef. From here it continued down the slope through a series of holes to a small cave at the base of a large rock. The hose was thus effectively concealed for a distance of approximately 30 yd from the cave.

Eight tests were conducted under various velocities of tidal current over a 15-day period

with no more than one trial on any one day. Each test was preceded by a 30-min control period during which any unusual behavior in sharks sighted was noted. The duration of the introduction varied according to the response of the sharks. Observations included the species and general behavior of the sharks and particularly the direction and nature of approach. The results are given in Table 2.

A consistent response was exhibited by both grey and blacktip sharks during this experiment. In the presence of a current they appeared from downstream, swimming at an accelerated rate directly to the mouth of the cave where, in most cases, they briefly stuck their snouts inside. They then turned in very small circles here for a short period of time before returning slowly, in a random manner, downstream. After an initial approach by any one shark, this same shark often reappeared and repeated the above described pattern several times. However, upon the third or fourth approach by the same shark, this shark often reversed direction 5–10 yd short of the hole and returned downstream without the characteristic circling.

TABLE 2
RESPONSE OF SHARKS TO EXTRACTS OF FISH FLESH OR SKIN (EXPERIMENT III)
(All Sharks Came from a Downstream Direction)

TRIAL	EXTRACT	TIDAL CURRENT	NO. AND LENGTH OF SHARKS RESPONDING	TIME TO INITIAL APPEARANCE	TOTAL INTRODUCTION TIME
1	frozen flesh	ebb, moderate	1 6-ft grey 1 4-ft grey 1 4-ft whitetip	10 min	1 hr
2	frozen flesh	flood, moderate	1 4-ft grey 1 5-ft grey 2 4-ft whitetips	12 min	1 hr
3	frozen flesh	ebb, moderate	1 4-ft grey 1 5-ft grey	25 min	30 min
4	frozen flesh	ebb, weak	1 4-ft grey 1 4-ft whitetip	35 min	1 hr
5	frozen flesh	ebb, weak to moderate	1 4-ft grey 1 4-ft blacktip 1 5-ft whitetip	16 min	45 min
6	frozen flesh	flood, moderate to strong	3 4-ft greys 1 4-ft whitetip	9 min	45 min
7	fresh flesh	flood, strong	2 6-ft greys 1 4-ft grey 1 4-ft whitetip 1 5-ft whitetip	7 min	30 min
8	fresh skin	flood, moderate to strong	3 6-ft greys 1 4-ft grey	6 min	30 min

It might be suggested that the olfactory stimulus had not itself been directional, but that the sharks, having been alerted by the olfactory cue, had simply turned upstream, and oriented to the current. However, while a rheotactic response may have influenced the shark in its initial decision as to which way to go in the corridor, this observer does not feel that the response observed could have been directed by such a cue. Among other considerations, in an approach directed solely by current the shark would have at least briefly overshot the source of the olfactory stimulus. This would have resulted in a brief but certainly noticeable period of uncertainty as the shark turned back to pick up the olfactory cue once again. Nothing of this sort was seen. Furthermore, the following of an olfactory corridor was observed in the absence of current and will be described shortly.

Occasionally the extract elicited a response from other fish in the area which could have provided an approaching shark with supplementary cues. However, in only 2 of 27 observed approaches might this source of error have affected the results.

When the current subsided, the approach of the sharks immediately became less direct—illustrating the importance of the current in maintaining the definition of the corridor. No new sharks appeared during slack water and those already present milled about continuously within 30 yd of the cave. Approaches to the cave during slack water were made in a random manner and from all directions. At this time it was apparent that the material was diffusing out in all directions from its source and was at the same time being retained in the immediate area.

The whitetip did not seem to be as responsive to the introductions as were the blacktip and the grey. On several occasions whitetips swam directly to the cave in the manner noted in the grey and blacktip. However, whitetips just as often swam past the hole without any noticeable response to the extract. As apparent unresponsiveness has been noted as characteristic of the whitetip, it is difficult to draw any direct comparisons between this species and the grey and blacktip from the observed behavior.

Whitetips do have the ability to follow an olfactory corridor. The following quotation from

the field notebook describes an incident which clearly illustrates this and also the formation of a corridor in the absence of current:

A large parrot fish (*Scaridae*, 10 lb.) was speared in about 20 ft. of water. The fish tore itself from the spear and took shelter in a large coral head. Within 1 min. a 5 ft. whitetip appeared. It became obvious that the shark had sensed the presence of the wounded fish as it poked about the holes of the coral head and then swam into one of them. The chase which followed was witnessed from the surface. The two fish could periodically be seen through one or another of the many holes which honeycombed the coral head. First the parrot fish would flash by and then the whitetip in pursuit. The coral head contained an extensive network of caves and the chase seemed to take advantage of most of them. Suddenly the parrot fish emerged from a hole. Apparently it had temporarily eluded the whitetip because there was no immediate sign of the shark. The parrot fish swam off rapidly on a straight course for about 30 yd. where it made a 90° turn and continued on the new course, in a straight line, until it was out of sight. The whitetip emerged from the hole just seconds after the parrot fish, but already its prey was out of sight. The whitetip circled briefly, then started out along the same path taken by the parrot fish. When it arrived at the point of the 90° turn it continued on a few yards, but quickly slowed and turned around. After another brief period of circling the shark picked up the second leg of the trail and followed it straight out of sight.

In this instance, the corridor was formed by olfactory substances given off by the moving wounded fish. There was no noticeable current at the time.

The sharks involved in Experiment II had apparently been initially alerted by an olfactory stimulus emitted by a fish which, while in distress, was uninjured.

The ability of these sharks to detect the presence of an unwounded fish in a state of stress through an olfactory cue was noted by Tester (1963) early in the program. This point has been neglected since the observations of Sheldon (1911), in which a dogfish was noted to locate an undamaged crab wrapped in eelgrass. However, in Sheldon's experiment the attracting stimulus (or stimuli) may have been a movement or sound made by the crab instead of, or in addition to, an olfactory stimulus. Any conclusions derived from Experiment II are open to the same criticism. Another source of criticism might be the assumption that a fish with a line passing through its maxillary membrane may be considered uninjured. The ex-

TABLE 3

RESPONSE OF SHARKS TO WATER CONTAINING A GROUPER UNDER STRESS (EXPERIMENT IV)
(All Sharks Came from a Downstream Direction)

TRIAL	TIDAL CURRENT	NO. AND LENGTH OF SHARKS RESPONDING	TIME TO INITIAL APPEARANCE	TOTAL INTRODUCTION TIME
1	flood, moderate	2 5-ft greys	15 min	30 min
2	ebb, strong to slack	3 4-ft whitetips	5 min	30 min
3	flood, moderate	1 4-ft grey 1 3-ft whitetip	10 min	1 hr

periment described below was designed to minimize these sources of error.

Experiment IV

This experiment was conducted to determine if these sharks are capable of detecting and tracking down, exclusively by olfaction, an uninjured fish under stress.

The experiment was carried out using the procedure described for Experiment III, except that, in place of the extract solution, the large plastic container was filled with sea water and contained an uninjured grouper (1–10 lb) which was presumably under stress. In each case, the fish was caught by line with a barbless hook. During the experiment the fish was agitated intermittently with a pole, using care not to inflict any damage, while the water was running from the container to the bottom as described for Experiment III.

Three trials were conducted over a period of 10 days, with at least 3 days between each trial. The results are given in Table 3.

The response was essentially the same as that to the extracts in Experiment III. Greys and whitetips were involved in the experiment; no blacktips were seen.

The captive grouper obviously emitted an olfactory stimulus which attracted the sharks upstream to the cave. Critics of this experiment may question whether a recently hooked fish can be considered uninjured. There is justification for pointing out the hook wound as well as the skin rubbed and mucus dislodged during handling. These factors offer a possible source of error. However, the results were consistent with findings in the laboratory tanks where it was possible to maintain considerably more control

over experimental conditions. In the latter tests (Tester, 1963) the strength of the stimulating olfactory component varied with the degree of distress of the fish being used. It appeared that a maximum level was reached shortly after the death of the fish.

It has been shown that the sharks were able to track down a distressed but apparently uninjured fish by olfaction alone in Experiment IV. Although they could also have made exclusive use of the olfactory sense in tracking down the hooked fish in Experiment II, it is highly unlikely that they did so. We shall see that, in all probability, other sensory modalities not only contributed to, but in fact dominated, certain phases of the approach.

RESPONSE TO COMPRESSION WAVES

Compression waves are regarded by many to have an important effect on the behavior of sharks, both as an attractant and as a repellent. Wright (1948) claims that attack patterns in sharks are released by sounds. Many investigators (e.g., Eibl-Eibesfeldt and Hass, 1959) report that the vibrations and sounds made by a wounded fish will attract sharks. On the other hand, some sounds have been reported to have a repelling effect, as for example the underwater shouts of divers (Hass, 1951). These reports are based on incidental encounters with sharks and are generally complicated somewhat by the presence of stimulating factors other than compression waves which might themselves have been influential in eliciting the observed response. For example, Wright's conclusion is based to a considerable degree on observations of sharks appearing just after an underwater explosion to feed on the dead and stunned fish.

The presence of the disabled fish is mentioned almost incidentally, although in such a situation it is impossible to dismiss the olfactory and visual cues emitted by these fish. Similarly, the presence of olfactory and visual cues also complicate reports of sharks being attracted to a struggling fish in response to compression waves. In regard to the repelling effect of the shouts of divers, we did not see any such response in the species studied in Eniwetok. However, sudden movements and/or a sudden burst of bubbles from the aqua-lung, such as might readily accompany a shout, often startled the blacktip and put it to flight.

It is important to consider the ability of sharks not only to sense these stimuli but also to locate their sources. Parker (1912), investigating sound as a directing influence on the movements of some teleosts, noted that there was a directing effect only during the duration of the sound. These results cast some doubt on the ability of such noncontinuous stimuli as a single underwater explosion to attract sharks.

Two experiments on the perception of compression waves by sharks were conducted in the field at Eniwetok.

Experiment V

The aim of this experiment was to investigate the effects of compression waves of a variety of sonic frequencies on these sharks. The following were presented:

A. Continuous pure tones, covering a frequency range in steps from 100–1,000 cycles per sec.

B. Sounds of mixed frequencies recorded on a circular tape, including:

1. wood struck against wood, 1/sec and 6/sec;
2. rock struck against rock, 2/sec and 6/sec;
3. rasping effect, continuous;
4. rattling of nuts and bolts in a bottle, continuous.

C. Shouts by the observer, directly projected through the apparatus.

The experiment was conducted at the Engebi location, using a tape recorder equipped with an underwater speaker lowered 6–8 ft below the surface. Each sound was presented during 20-min trials, with each trial immediately following a 20-min control period and conducted

under two sets of conditions: (1) following a different experiment in which sharks had been drawn into the experimental area and were still present, and (2) upon arrival at the site, with no sharks present. All sounds were audible to a submerged human at distances greater than 150 ft.

Although we watched closely for signs of any sort of response, for example curiosity, we saw nothing in the behavior of the sharks which suggested that they were able to perceive the sounds.

Experiment VI

This experiment was designed to investigate the effects of various subsonic compression waves on these sharks.

A metal hoop, having a diameter of 36 inches, was fitted with a rubber diaphragm held in position by a series of surgical tubing lacings. This piece of apparatus was installed midway through a natural tunnel, approximately 20 ft long, in the coral ridge bordering Deep Channel beneath the raft. A line was secured to the center of the diaphragm on that side facing away from the channel, and this line was run out of the tunnel and up to the surface where a small skiff rode at anchor. The diaphragm could thus be vibrated by jerking on the line.

Two trials were conducted in which the diaphragm was vibrated irregularly for a period of 20 min immediately following another experiment in which a number of grey sharks had been drawn into the area and were still present. Throughout both trials there were grey sharks swimming about calmly in the area. At times they passed within 5 yd of the tunnel's entrance.

In observations from the raft we looked for any type of response in the sharks which might indicate that they were aware of the vibrating diaphragm. We saw no such response.

The negative results in these two experiments do not mean that the sharks could not perceive these stimuli. If releasers of feeding activity are emitted by struggling fish in the form of compression waves, they probably are of a specific nature or involve a characteristic pattern. It would have been a rare stroke of luck if we had duplicated a specific releaser with our crude experiments. The problem of delimiting the

sensory capacity for stimuli of this sort is probably best approached with conditioned response experiments on captive sharks under controlled conditions before attempting to establish their role in feeding behavior under natural conditions.

Although the work of Parker (1903, 1911), Kritzler and Wood (1961), and others has demonstrated that at least some sharks are sensitive to compression waves of a relatively wide range of frequencies, it has yet to be proven experimentally that such stimuli normally release feeding behavior. Nevertheless, incidental observations at Eniwetok indicated they do play an integral role in feeding activity. These observations are of a nature similar to those mentioned at the beginning of this section and are subject to the same reservations. One such observation is quoted from the field notebook:

... A 30 lb. grouper was speared on the slope bordering Deep Channel ... the grouper fled, dragging the spear, into a small cave. ... Within seconds, 5 greys 4-7 ft. in length swam excitedly into the area from downstream. As soon as they were in the area, however, their excited state diminished. They swam about in the area for several minutes, appearing to steadily lose interest, before slowly drifting off downstream and out of sight. After a few minutes ... 5 greys made another approach which seemed as highly motivated as the preceding one. Immediately I looked below to see a small puff of sediment emerge from the cave—the grouper was obviously thrashing about inside. Almost as soon as the sharks were in the area, all became quiet in the cave, whereupon the sharks immediately lost their excited state and settled down to cruising about as before. Two 4-ft. whitetips joined them before they all again drifted off downstream. After a few minutes ... another small puff of sediment was visible at the mouth of the cave—the grouper was struggling again. I quickly looked downstream to see the greys on their way in as before. The pattern previously described was repeated, but this time there were 4 whitetips (3-5 ft.) in addition to the 5 greys. Several minutes after the sharks disappeared downstream for the third time the grouper scrambled out of the hole and, dragging the spear, struggled along the bottom toward the bigger, more protective caves farther up the slope. The 5 greys charged into the area from downstream before it had gone 20 ft. At this point, the grouper stopped, and ceased all movement. Although the grouper was in a completely exposed position, the excited state of the onrushing greys diminished almost as soon as the grouper stopped moving. Instead of attacking the completely vulnerable grouper as I expected, the greys settled down to swimming slowly and randomly about the area. Often they came within inches of the mo-

tionless grouper, and on at least one occasion grazed it. The 4 whitetips rejoined the group, along with 2 blacktips (3 and 4 ft.) making a total of 12 sharks, all obviously interested, but offering no show of excitement or indication that they regarded the wounded grouper as prey. Nevertheless, the sharks did not gradually drift off downstream as they had previously, but continued to swim about in the area. Thirty minutes later, when we had to leave, the situation was unchanged—the grouper was still sitting motionless in the same spot, while the 12 sharks swam slowly about. Most of this random swimming about the area, both at this point and earlier, had occurred downstream of the grouper.

It was significant that all approaches and departures, as well as most of the random swimming in the area, occurred downstream of the grouper. This indicated that olfaction was involved throughout the incident. Although the excited approach of the greys during this incident appeared to coincide with the periods when the grouper was struggling, it is possible that they had first been conditioned by an olfactory cue. In this case, the olfactory cue may have had a threshold lowering effect for the postulated compression wave stimuli. At least one author (Wright, 1948) doubts that olfaction alone will release attack patterns in sharks. In this latter regard, blinded sharks in the tanks fed avidly on chunks of fish flesh which were lying on the bottom, thus offering little other than olfactory stimuli before the sharks came into contact with them. The question here is whether or not the behavior of these blinded sharks can be considered normal.

While the sharks in the latter phase of the incident did not attack the wounded grouper, they did not drift off downstream as they had done when this same fish was concealed in the cave. We are probably safe in assuming that the behavior pattern demonstrated in swimming slowly about in the area was appetitive in nature. This suggests that an additional stimulus was required to release the actual attack. This is to say that a combination of stimuli, e.g., an olfactory element and erratic motion might have been necessary to release the attack in this case. The olfactory cue may have simply released an exploratory behavior pattern which drew the sharks to the area. Once there, the release of the attack may then have required a specific stimulus not presented by the quiet, natural looking grouper, the coloration of which blended

in very well with the bottom on which it was resting. The cessation of movement by this grouper upon the approach of the sharks may have been a well-established protective behavior pattern. We will consider this incident further in the next section. During a later period of the study, a grouper of the same species and approximately the same size was caught at the raft where the underwater action was witnessed from the observation cage. The grouper wrapped the line about a piece of coral and by the time the line was freed and the struggling fish hauled toward the surface, a single 5-ft grey came rushing into the area from downstream. The shark went directly for the struggling fish, took the tail section into its mouth, and with a few vigorous lateral shakes of its head came away with the after portion of the fish.

There is no doubt that rapid erratic movements are a prime releaser of attack patterns in these sharks, particularly in the presence of specific olfactory cues. Many authors have noted an excited state in sharks resulting from the sensing of movement (for example Limbaugh, 1958). As both a mechanical disturbance and a visual stimulus are usually produced by a moving object underwater, it is very often difficult to say with certainty which is more significant as a releaser of attack in a given situation.

On one occasion, while fishing for sharks, a 3-ft grey was hooked in the presence of five larger greys. As the shark struggled vigorously on the line, the other five sharks became highly active and appeared to be chasing the hooked animal. Initially we supposed that an attempt was being made to attack the hooked shark, but upon landing this individual after several minutes of activity we noted no evidence of injury. If the larger sharks had been attempting to feed on the smaller hooked shark there is no doubt that they could have done so. It is probable that the activity of the hooked shark excited the others which were then simply following the focal point of this activity. Inasmuch as other species of fish, similarly hooked and struggling, were immediately taken by the grey shark there is a suggestion here that this species of shark is inhibited in some way from attacking members of its own species. This possibility is further supported from observations made while fishing for snapper (*Lutjanus bohar*) at Palmyra. Grey

sharks drawn to the fishing area showed no interest in the many free-swimming snapper, but would immediately attack a snapper which became hooked and began to struggle on the line. Contrariwise, although the sharks would swim rapidly about one of their own species which was hooked and struggling, no attacks were observed.

RESPONSE TO VISUAL STIMULI

Contrary to many reports on the subject (for example Halstead, 1958) vision was found to play a major role in the feeding activity of the sharks in the Eniwetok lagoon. We briefly mentioned vision above in regard to instances involving movement. The following experiments were designed to further clarify the role of vision in cases where there was little or no movement of the bait.

Experiment VII

The object of this experiment was to determine the role of vision in these sharks when they are approaching a motionless bait up an olfactory corridor.

Two baits of similar appearance were prepared for each trial, one of which was a 4-inch cube of grouper flesh while the other was a 4-inch cube of wood. After we were confident that no sharks were visible in the area, the two baits were presented together in a strong current, suspended 3 ft apart, midway between the surface and the bottom. Observations were made from the cage, and a record was kept of which bait was hit first, as well as of the nature and direction of approach of the sharks.

Experiment III had shown that these sharks are capable of orienting on an olfactory stimulus in a current and swimming directly to its source. In every case during the present experiment the sharks appeared from downstream, swimming at an accelerated rate, presumably following an olfactory trail emitted by the grouper flesh. If the sharks had continued to orient exclusively on the olfactory stimulus all the way to the bait, then the fish would presumably have been taken in all trials. This, however, did not occur. In 20 trials conducted over a period of 2 days, the fish was struck first 11 times while the block of wood was hit first 9 times. As no preference was

shown, it seems that at least the final phase of the approach was visually directed.

When the shark selected the wood, the object was either simply bumped or briefly taken into the mouth and then rejected. No teeth marks were found on the wood following the test. In all cases the fish-baits were carried away. Only grey sharks were involved.

If we accept as fact that these sharks orient visually during the final phase of their approach to a motionless prey, we must then question the nature of the stimulating visual image, bringing us to the subject of visual acuity.

Most elasmobranchs reportedly possess an all-rod retina with a high ratio of visual cells to ganglion cells, which provides for low visual acuity. While this would presumably result in an inability to see objects in detail, the sharks would be able to utilize their visual sense under conditions of relatively little light (Gilbert, 1961). Kato (1962) found no evidence of cones in the retina of blacktips or whitetips. Perhaps even more significant, he found no specialized area, corresponding to the human fovea, which is generally assumed to be associated with visual acuity.

At Engebi, we often noted that sharks attracted by a dead fish suspended on a line often struck objects in the immediate vicinity of the bait before taking the bait itself. A rock about 1½ ft square, which was situated in the middle of a sandy area below the baits, as well as floating seaweed and a lead weight on the line a foot above the bait were often tested with a nudge or by actually being taken momentarily into the mouth. These observations suggest one of two alternatives: (1) these sharks lack the visual acuity necessary to distinguish the visual appearance, i.e., form, markings, etc. of fish from inedible objects in the immediate vicinity; or (2) although these sharks do possess the visual acuity necessary for such a distinction, it was not utilized by them in this situation.

Tester and Kato (MS) showed that small blacktips and greys have the ability to discriminate between a number of objects of different shape, e.g., squares, triangles, and rectangles, and that they make this discrimination from a distance of at least 6 to 12 ft. These species then possess at least the degree of visual acuity required to discriminate between these forms.

The following experiment was an attempt to detect evidence of the utilization of a high degree of form discrimination ability in the feeding behavior of these sharks.

Experiment VIII

This experiment was designed to determine whether or not the visual cues offered by a fish through its characteristic morphological features are significant attractive visual stimuli to these sharks.

Two fresh dead fish were selected for each trial, both being of the same species, but one a little larger than the other. Three species were used: goatfish (Mullidae), 8 trials; surgeon fish (Acanthuridae), 3 trials; and squirrel fish (Holocentridae), 10 trials. The larger fish was then decharacterized by removing the head and all the fins, reducing it in size to approximately that of the smaller, still natural-appearing fish. A long, deep incision was then made along the ventral side of the natural-appearing fish to insure that olfactory stimuli emitted by both baits were essentially the same. The baits were both secured to a single line, one spaced approximately 18 inches above the other, with their respective position being reversed on alternate trials. After assurance that no sharks were visible, the baits were suspended motionless at a point midway between surface and bottom in a strong current. Observations were made from the cage and a record was kept which bait in the pair was taken first, along with the species of shark involved and the nature and direction of approach.

It was assumed that if the characteristic morphological features which had been removed from one of the pair were significant as attractive visual stimuli, then the natural-appearing fish would be favored in the initial choice made by the sharks. This in turn would demonstrate a high level of form discrimination ability in these sharks. However, no apparent preference was shown to either of the two bait types in 21 trials. The decharacterized fish were hit first 11 times, while the natural-appearing fish were hit first 9 times. Once both baits were hit simultaneously. The relative positions of the baits on the line had no apparent effect, with the top bait being hit first 9 times and the bottom bait

11 times. As in Experiment VII, only grey sharks were involved and these approached in every case at an accelerated rate from downstream. By positioning the bait in mid-water we favored this species. A number of whitetips were seen about the bottom at various times during the trials.

The baits introduced during this experiment were the first food given by us to the sharks in over a month, with the exception of a few uninjured living fish. This is an important consideration in this experiment, as any conditioning of the shark population to feeding on our presentations would have resulted in a tendency to take our offerings indiscriminately. However, no conditioning was noted at this stage of experimentation.

The failure of these sharks to show a preference for the natural-appearing fish over the one which had been reduced to a simple object suggests that the visual appearance of a fish per se is not itself significant to these sharks when feeding. When the results of this experiment are considered along with the observations at Engebi already mentioned, in which the sharks struck at inedible objects in the immediate area of the baits, it appears that the significant visual cue in these cases was simply that of an object within the immediate area of the source of the olfactory stimulus. This evidence suggests that these sharks do not utilize a high degree of visual acuity in their feeding activity. It follows, then, that if the visual stimulus is not moving, it must otherwise contrast with the background against which it is viewed in order to provide an effective visual cue.

The following experiment involves the relative effectiveness of two objects in attracting the attention of sharks, when these objects differ from one another in degree of contrast in brightness with their background.

Experiment IX

This experiment was designed to determine which of two baits, one white and the other black, would be taken first when both are presented to these sharks together at the surface.

Paired 3-inch cubes of fish flesh (parrot fish, snapper, and grouper) were used as bait in this experiment, with members of each pair identical

except that one retained its natural white color, while the other was dyed black with nigrosine dye. It had been previously determined that nigrosine dye was not sensed by blinded sharks in the tanks.

The experiment was conducted at the raft over 40 ft of water when a current was running. A wounded grouper was placed in the cage until a number of sharks had been drawn about the raft. The fish was then removed from the water, allowing the source-point of the olfactory stimulus to be carried off downstream and taking the sharks with it. When the sharks were about 20 yd downstream from the raft, the two baits were dropped into the water, spaced approximately 10 ft apart. Movement of both baits was negligible as they slowly settled. At times the response of the sharks immediately followed the entry of the baits into the water, indicating that the splash had been sensed; at other times the response was noted after the baits began to sink, indicating a visual response. These responses followed the introduction too closely to have been those of olfaction. In either case, the sharks came racing back upstream and in all cases the baits were taken before they had fallen 10 ft. The bait taken first in each case was recorded, although the alternate bait was always taken almost simultaneously. As it was anticipated that the amount of incident light present would influence the results, trials were conducted under different light conditions, with from 10 to 56 trials held each day for 4 days.

The results under each of the different sets of conditions prevailing were as follows: (1) daylight with clear sky, in 96 trials black was taken 79 times, or 82%; (2) daylight with overcast and drizzle, in 21 trials black was taken 15 times, or 71%; (3) daylight with overcast and heavy rain, in 14 trials black was taken 8 times, or 57%; (4) after sunset, with clear sky but almost dark, in 41 trials black was taken 32 times, or 78%. The total: for 172 trials under all conditions, black was taken 124 times or 72%.

As the sharks, all greys, raced back toward the test area they were viewing the baits against light surface water. The black bait, then, contrasted with its background to a greater degree than did the white bait. This was as noticeable

to the observer sitting in the cage as it obviously was to the sharks.

Recalling some of the observations made earlier, we might consider again the speared grouper which rested motionless on the bottom while 12 sharks swam slowly about in its immediate area. Although this grouper was in a completely exposed position, its coloration blended in well with the bottom on which it was resting. In this position the grouper was apparently at least temporarily safe from attack by the 12 sharks, in spite of the fact that it was wounded and still emitting the olfactory stimulus which presumably had released the appetitive behavior pattern which these sharks were at that time demonstrating. At Engebi, the sharks struck at the rock which was sitting in the middle of the sandy area, floating seaweed, and the lead weight—all inanimate objects in the immediate area of the bait, but all of which sharply contrasted in brightness with the backgrounds against which they were viewed by the sharks. These results are consistent with the conclusions drawn by Gilbert (1961) from anatomical studies of the shark eye.

Although there is little doubt that vision is the predominant directing sense within the visual field, the effective distance involved here will be highly variable. Such external factors as water clarity, incident light, and whether or not the prey is under cover, no doubt determine the effectiveness of vision in any given situation.

RESPONSE TO GUSTATORY AND TACTILE STIMULI

While lack of visual discrimination apparently led to selection of the wood as often as it did the fish during Experiment VIII, the shark was quick to learn its error. Initially the wood was actually taken into the mouth, but after one or two successive trials a nudge was generally sufficient to dismiss the inedible object. An appraisal of the bait by the visual or olfactory sense may have been the basis for the nudge, but when the bait was taken into the mouth, other senses, e.g., gustation and/or tactile sense, undoubtedly came into play.

A review of the gustatory sense of sharks is presented by Tester (MS). In this review, he points out that while the receptors of the gus-

tatory sense (e.g., taste buds or terminal buds) occur in the skin of the body, fins, and barbels of many species of fishes, in the elasmobranchs they appear to be associated with papillae which are confined to the epithelial lining of the mouth and pharynx. He also calls attention to the claim of Budker (1938) that the "pit organs" located on the body of elasmobranchs have a gustatory function.

An effort was made to design an experiment which would illustrate the respective roles played by both gustation and the tactile sense in accepting or rejecting food taken into the mouth. As the block of wood in Experiment VIII differed from the fresh fish in tactile cues as well as those of olfaction and gustation, it was impossible to say which of the two might have been more influential in the rejection of the wood.

An attempt was made to synthesize a bait which possessed the visual and tactile properties of acceptable bait, but which lacked the olfactory and gustatory properties. Tester et al. (1955) concluded that in the flesh of many fishes there is present a substance or substances which, when extracted with alcohol or water, can be perceived by a fish through its sense of smell or taste and which promotes the urge to feed. Tester commented (personal communication) that extraction by alcohol was effective in removing this substance from a piece of flesh. He observed that squid prepared this way was not detected by blinded blacktips and although taken into the mouth by normal blacktips, they were subsequently rejected. He attributed this rejection to the lack of acceptable gustatory stimulation, in as much as the texture of the prepared squid seemed to be similar to untreated squid.

The following experiment was an attempt to duplicate Tester's results in the field.

Experiment X

This experiment was designed to determine whether or not a bait offering the visual and tactile stimuli of food, but which lacks the olfactory or gustatory stimuli, will be acceptable as food by these sharks when they are actively feeding.

A number of 3-inch cubes of grouper flesh

were prepared. Half of these baits were soaked for 4 days in each of the following concentrations of ethyl alcohol: 35%, 75% and 95%, in that order. After the alcohol treatment the baits were soaked in sea water for 3 hr. It was hoped that the product of this process would be a bait which felt and looked like food, but did not taste or smell like food. In actuality, however, the texture of the product was not identical to that of normal flesh, being notably dry and leathery. The experiment was nevertheless continued, with each of the treated baits being paired with a normal bait. It was assumed that the normal bait would be taken. If the treated bait was also taken this would indicate that the wood in Experiment VIII had been rejected due to its tactile properties rather than its lack of acceptable olfactory or gustatory stimuli. If, however, the treated bait was not taken, Tester's results would be confirmed and it would appear that gustation (and perhaps the tactile sense too) had been involved in the rejection of the wood.

The test was carried out at the raft, in a moderate current, using essentially the same technique described for Experiment IX, except that in this case all 15 trials of the experiment were conducted during a 30-min period of one afternoon and the response to both baits was noted.

Only grey sharks were involved in the results. The treated bait was hit first 6 times, while the natural bait was hit first 9 times, indicating that the sharks did not make a distinction between the visual appearance of the two baits. All the baits were taken into the mouth, but although in all trials the natural bait was swallowed immediately, the treated bait was rejected within seconds. As this rejection took place after the bait had been taken into the mouth, it appeared to be based on gustatory stimulation (if we are correct in assuming that the bait offered acceptable tactile stimulation). A snapper was seen taking, and apparently retaining, one of the treated baits rejected by the grey shark.

Another effort to clarify the roles played by gustation and the tactile sense in feeding involved the use of sponges. It was thought that perhaps a sponge which had been soaked in an extract of fish flesh would be accepted by the sharks as food. If this were the case, then by pairing the soaked sponge with a normal sponge

it would have been possible to present a choice of baits which posed the same problem to the sharks as did Experiment X. In order for the experiment to have been a success, however, it was necessary for the sharks to have accepted the soaked sponge as food, and this proved to be only temporarily true. Initially, the soaked sponge was carried off in the manner seen with a chunk of fish, while the plain sponge was rejected as was the prepared bait in Experiment X. However, after 3 trials the sharks began to lose interest in the soaked sponges until they either dismissed them after an unenthusiastic nudge, or ignored them completely. Furthermore, as the sharks learned that the soaked sponges were inedible, the extract no longer excited them. In this latter regard it is difficult to say whether the sharks actually learned that the extract did not indicate food or whether olfactory fatigue was the major factor.

A definite change in general behavior of the grey sharks was first noted during Experiment IX and became very evident during Experiment X. As the sharks became conditioned to feeding about the raft they responded instantly to any object which was presented. In addition, there was a sharp increase in the number of sharks responding to our test situations. Where initially a maximum of 5 or 6 grey sharks were involved in our experiments, the number steadily increased during this period of increased food supply until more than 20 were being drawn about the raft. The initial population had been relatively stable and through successive observations involving experiments which utilized minimum feeding, it had become possible to recognize a certain group of about 6 individuals that appeared day after day. These same individuals were seen after the population numbers increased, but apparently many other sharks which normally frequented other areas were drawn to this point of concentrated feeding. This change involved only grey sharks, which is understandable as this species was completely monopolizing the additional food. The increase in numbers of sharks resulted in a markedly increased element of competition. When we witnessed the simultaneous rush at the baits by up to 10 sharks, it was understandable that all baits were taken into the mouth before any discriminations were made as the slightest hesitation by

a shark in this situation immediately eliminated it from a chance at a bait. Fortunately the present tests, which required concentrated feeding, were concerned with probing questions which did not suffer from these effects. This change in behavior, along with the increase in numbers of the local sharks, was therefore viewed with interest rather than alarm.

FOOD PREFERENCES

Sharks have been popularly described in a general way as creatures with an exceptionally voracious appetite, feeding on such unlikely objects as tin cans, bottles, and other trash (Lineaweaver, 1960). Although considerable effort was brought to bear on the problem of food preferences during this study, the experiment described below was the only one, of many experiments conducted, which clearly indicated a preference for one of two food materials presented.

Experiment XI

This experiment was an effort to determine whether or not these sharks show any preference between grouper flesh and the flesh of various species of mollusks, e. g., *Tridacna* sp., (10 trials); *Spondylus* sp., (5 trials); and *Cassus* sp., (3 trials).

Mollusk flesh in 2-inch cubes was paired with chunks of grouper flesh of the same size, with both baits thus offering an essentially identical visual appearance. Prior to the test, large pieces of grouper and mollusk flesh of the species to be tested were placed in the cage on the raft to attract sharks. When the introductions began, there were 10 grey sharks, 3 to 6 ft in length, present in the area. The method of introduction was as used in Experiments VIII, IX, and X, except that all trials were conducted during one session. Observations were made to detect any evidence of a preference which might be shown between the two baits.

The fish baits were hit first 8 times, while the mollusks were hit first 9 times, indicating that there was no visual preference. However, although both the fish and mollusks were taken into the mouth with equal vigor, the fish were presumably swallowed while the mollusks were rejected almost immediately. The results were comparable to those of Experiment X, with the

response toward the mollusks similar to that shown toward the treated bait. On one occasion a single shark took the *Tridacna* and then the grouper. After a short period, with both baits in its mouth, the shark rejected one, presumably the *Tridacna*. These same rejected baits were subsequently taken by groupers and snappers which waited below the feeding sharks. Although the mollusks tested were unacceptable as food by these sharks, it is known that they will feed readily on squid.

It was possible, therefore, to observe a preference when one of the bait-choices offered was unacceptable to the sharks. However, when both bait-choices presented were acceptable, it became difficult to make this distinction, even though one might have been significantly more attractive than the other. Thus, most of our experiments concerning food preferences yielded inconclusive results. For example, a test might have been conducted to determine the comparative attractiveness of two baits, A and B, both motionless and presented on the lines within 10 ft of each other. As indicated in Experiment VIII, although these sharks might have been drawn in by an olfactory stimulus produced by bait A, they would then have been quite likely to have hit B inasmuch as the final phase of the approach to the bait would have been visually directed. Once having taken bait B, this bait would be retained as long as it was not actually unacceptable.

It has been noted (Tester, 1963) that some types of fish flesh appear to be more attractive to sharks than do others. In the ponds at Coconut Island the notably dry-fleshed snapper, *Lutjanus gibbus*, appeared to be far less desirable to captive sharks as food than did the much juicier tuna, *Katsuwonus pelamis*. Springer (1958) also noted this preference for tuna. Is it possible that this apparent preference is actually due to a higher concentration of some basic attractant which is common to the flesh of both fish? It has become increasingly apparent that some substance (or substances) in fish flesh is perceived by the sense of taste and/or smell of these sharks which is a powerful element in the release of a highly motivated feeding pattern. Furthermore, it was indicated in Experiment X and also in the work of Tester et al. (1955) that this substance could be ex-

tracted from the flesh, whereupon the flesh itself was left undesirable to the sharks. Tester et al. (1955) expended considerable effort in attempts at purification, fractionation, and identification of the attractant extracted from fish flesh which released a response in captive tuna. While the precise identity of the substance eluded the investigators, many of its chemical properties were determined and presented by the authors. Tester et al. (1954) suggest that the so-called attractant which is present in the body juices of fish, squid, shrimp, and other forms may be a substance (or substances) which is common to all these forms.

FEEDING DETERRENTS

The recent increased interest in the habits and behavior of sharks has stemmed largely from a growing awareness of the need to develop a more effective means of protecting humans from shark attack.

A number of tests of proposed repellents were conducted, including a test of the repellent now in general use by the armed services. The results of some of these tests illustrate many of the problems involved in producing an effective repellent.

Experiment XII

This experiment tested the effectiveness of the standard shark repellent (copper acetate-nigrosine dye) in protecting both dead and wounded fish from attack by these sharks.

The experiment was conducted at two locations: (1) on the bottom at the edge of Deep Channel, and (2) from the raft. In the tests on the bottom, involving whitetips, three baits were tied to packages of repellent and anchored on the bottom, while seven baits, without repellent, were anchored nearby. In the tests from the raft, which involved grey sharks, all the baits were tied to packages of repellent and lowered halfway to the bottom. No attempt was made to attract sharks before beginning these tests.

The whitetips took all of the unprotected baits but did not take any of those tied to the packages of repellent. On the other hand, although the first grey to appear during the tests at the raft occasionally exhibited a slight hesi-

tation when making its approach, it was never long before several greys were in the area and the bait and repellent package were quickly taken together. The repellent packages were shortly rejected, but there was no indication of a subdued appetite. One grey was seen swimming away trailing a black cloud of shark repellent from its gills with no show of discomfort.

The relative effectiveness of the repellent in protecting the baits from the whitetips may be related, at least in part, to the absence of the group feeding effect in this species. This effect, which was discussed earlier, was noted to lower the threshold for the release of feeding patterns in grey sharks.

Experiment XIII

In this experiment the standard shark repellent was presented as a large cloud, both by itself and as a protective screen for various attractants. Trials were conducted at the raft in which 30 gm of repellent were dissolved in 64 gal of sea water in a plastic container. This solution was presented alone as well as mixed with each of the following attractant materials: (1) two small macerated goatfish, (2) 500 ml-fish extract, (3) 1,000 ml of fish extract, and (4) 2,000 ml of fish extract. The extracts were prepared by using 50 gm of grouper flesh per 500 ml of fresh water.

The presentation was made by simply pouring the contents of the container into the water after a number of sharks had been drawn in about the raft and noting the results. In each case, a cloud approximately 6 ft deep and 12 ft wide formed at the surface next to the raft and slowly drifted downstream.

When the plain repellent cloud was introduced, the sharks rapidly converged on the cloud to a distance of approximately 5 yd where they circled slowly, following the cloud as it drifted downstream. After a few minutes, however, the sharks lost interest in the cloud and returned to the raft. When the repellent cloud containing the macerated goatfish was introduced, the fish fragments sank beneath the cloud where they were quickly taken by the sharks. The sharks, then excited, swam unhesitatingly up into the cloud where they circled vigorously. Sixteen

greys, 3–6 ft long, were involved in the first two phases of this experiment.

The response to the repellent clouds containing the extract solutions was essentially the same in each case. After rapidly approaching the cloud, the sharks circled briefly about its edges and then moved slowly inside without notable excitement. Within 5 min of introduction, all sharks had lost interest in the introduction. Eight greys, 3–6 ft in length, were involved in these tests.

It seems noteworthy that the extract elicited an unexcited pattern of exploratory behavior rather than the highly excited aggressive behavior seen following the introduction of macerated goatfish. In any case, the most that can be said for the repelling qualities of the material used in this test is that the sharks did not swim into the cloud without incentive to do so. It may theoretically have served to conceal an otherwise attractive visual stimulus which might have been inside.

Experiment XIV

This experiment tested the effectiveness of an underwater light suspended on a line in protecting dead fish.

The apparatus was designed so that the bait (dead goatfish) was suspended 2 ft below the light in a position where both could be viewed from the underwater chamber. Observations were then made of the response of the sharks to the bait, both in the presence and in the absence of light. Tests were conducted during four different nights using both 110- and 300-watt bulbs. A steady light was used, as well as a light which flashed at rates of approximately 15, 35, and 50 flashes per min. Periods of light, 20 min long, were alternated with 20-min periods of darkness during both of which the baits were presented. Sharks had been drawn to the area by bait placed in a wire basket which was suspended in the water and then raised prior to each test. A strong current was flowing toward Deep Channel during each test.

Initially the steady light was effective in protecting the bait from the sharks for the entire 20-min period, with the bait being taken soon after the light was extinguished. During the early periods of light the sharks milled about

at the edge of the field, consistently downstream of the bait and light. Upon continued contact with the light the sharks became progressively bolder until despite the light, flashing or steady, they showed little hesitation in taking the bait. This boldness seemed to increase notably with the number of sharks present. There were usually between 5 and 10 grey sharks present during these tests; no other species was seen. This test proved to be a good illustration of progressive loss of apprehension through growing familiarity with an initially strange situation, as well as the mutually stimulating effect of some species of sharks on one another in certain situations.

CONCLUSIONS

1. Three species of sharks are common in Eniwetok lagoon: the grey shark, *Carcharhinus menisorrhoea*; the blacktip shark, *C. melanopterus*; and the whitetip shark, *Triaenodon obesus*.

2. Each species inhabits a rather characteristic habitat within the lagoon: (a) the blacktip in relatively shallow water (1–40 ft approx.) over sand and coral rubble flats which extend out from shore for distances ranging from a few yards to several miles; (b) the grey, along the outer slope of these flats, in deeper water and in the passages to the sea; and (c) the whitetip about rock-ledges and coral heads.

3. The feeding behavior of these sharks shows differences which in many cases appears to be associated with their characteristic habitats.

4. Blacktip and grey sharks show a marked increase in excitement when feeding in numbers. This phenomenon, often referred to as a "feeding frenzy" in extreme cases, does not seem to occur in the whitetip.

5. All three species are highly sensitive to stimuli emanating from or suggesting injured and/or distressed, as well as dead or moribund prey.

6. These sharks can detect, by olfaction, both injured fish and uninjured fish in a state of stress.

7. Olfaction is the most effective sense in detecting prey at a distance, providing the olfactory stimulus has had sufficient time and means for effective dispersal.

8. These sharks are able to follow an olfactory stimulus quickly and directly to its source without benefit of other orienting stimuli when the olfactory material has been drawn out as a narrow trail by a strong current or, in standing water, when the source of the olfactory stimulus is moving.

9. Generally, olfactory stimuli are effective in releasing a highly motivated pattern of exploratory behavior in grey sharks, which is appetitive in nature. Consummation of the feeding act then requires a subsequent specific stimulus, as for example one of vision.

10. The grey shark is often highly excited by, and attracted to, the source of rapid and/or erratic movement. The effect is intensified in the presence of certain olfactory stimuli but is not dependent on their presence.

11. Despite displaying varying degrees of initial curiosity toward many unusual stimulus situations arising in their environment, the sharks exhibit caution when encountering a situation which is unfamiliar. This caution will steadily subside, however, with an increasing familiarity with the situation.

12. The final phase of approach to a motionless prey by the grey shark is normally directed by vision, even though the feeding pattern may have been initially released by some other sensory modality, for example, olfaction.

13. Although vision is an important sense in the feeding activity of these sharks, a high degree of acuity and form discrimination is not demonstrated. Rather, the significant visual cues seem to involve the detection of movement or contrasting brightness, or both.

14. These sharks may attack any object which they sense in a high concentration of an olfactory material.

15. The grey shark rejects, from the mouth, food which does not permit acceptable gustatory stimulation.

16. The standard shark repellent (copper acetate-nigrosine dye) now in use by the armed forces is ineffective in preventing the grey shark from swimming into a cloud of this material when the species is present in numbers and is motivated by food within and adjacent to the material.

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Life History of the Caligid Copepod *Lepeophtheirus dissimulatus* Wilson, 1905 (Crustacea: Caligoida)¹

ALAN G. LEWIS²

COPEPODS of the family Caligidae are found as external parasites on both fresh and salt water fishes throughout the world. Even with their wide distribution, relatively little is known about their life history. The presentation of the life history of *Lepeophtheirus dissimulatus*, a caligid found on salt water fishes, should provide more information on the life history and general biology of this group of copepods.

Although there are many references to immature and juvenile or larval stages (reviewed by Heegaard, 1947: 21-31), only a few workers have had the material to describe the complete life history of a caligid. Through methods described below, the author was able to obtain a series of Hawaiian specimens representing all of the stages of development of *L. dissimulatus*.

Lepeophtheirus dissimulatus is one of the more common parasitic copepods of Hawaiian acanthurid (surgeon) fishes. The species is not limited only to Hawaiian fishes but is known from a wide variety of localities and a wide variety of hosts (Lewis, in press). Even with its wide distribution, in both the Atlantic and Pacific oceans, larval stages have been described only once, by Shiino (1959:309), from fishes of the Revilla Gigedo Islands.

Attempts to rear the copepod from the egg to the adult in culture were only partially successful. Ovigerous adult females were placed in clean finger bowls partially filled with cotton-filtered or unfiltered sea water. Circulation of the water was accomplished by means of a fine jet of air from a slender glass tube immersed in the medium. The water was changed at least once

every 8 hr and usually more frequently. At the time the eggs, carried by the female, hatched, a portion of the first nauplii, the first larval stage, was removed with a wide-mouthed pipette and placed in small stender dishes. The remaining nauplii were left in the finger bowl and the adult female was removed and placed in a separate bowl. Water in the finger bowls was circulated in the same manner as above and changed at the same time intervals. Water in the stender dishes was not circulated but instead was changed at more frequent intervals, every 3-4 hr. As moulting occurred into the second naupliar stage, the newly moulted second nauplii were transferred to new finger bowls or stender dishes except for three to four individuals which were preserved in either 10% buffered formalin or 95% ethyl alcohol. Shortly after the second naupliar stage moulted into the succeeding stage, the copepodite, a piece of loosely woven nylon cloth was placed in the dishes to offer a substrate for attachment. (It was found that the copepodite stage is the stage which attaches to the host.) In addition, pieces of host tissue were placed in some of the dishes. The host tissue was left in the dishes for 1 hr and then removed and the animals transferred to a new dish in order to reduce contamination and bacterial action.

The mortality rate between the first and second naupliar stages was high and appeared to be partially due to the inability of the nauplius to break out of the old cuticle. The rate from the second naupliar stage to the copepodite was relatively low. Out of the 30 attempts that were made to rear the copepod, each with at least one female carrying from 20-60 eggs, one copepodite was obtained that attached to the nylon cloth placed in the dish. The remaining copepodites died without attaching and the single copepodite that attached died immediately thereafter. None of the copepodites attached to the host tissue placed in the dishes.

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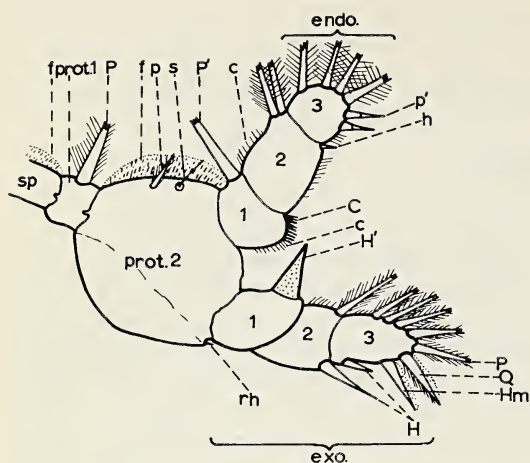


FIG. 1. Hypothetical thoracic leg of *Lepeophtheirus dissimulatus*, showing the various armament components. C, Heavy setae; c, fine setae; endo, endopodite; exo, exopodite; f, membrane; H, well-developed spine; H', laterally projecting spine appearing as a continuation of segment; h, poorly developed spine; Hm, membrane margined spine; P, large plumose setae; P', large naked setae; p, small plumose setae; p', small naked seta; prot, protopodite; Q, seta (or spine) plumose on one side and membrane-margined on other; rh, spinule; s, hairlike seta; sp, sternal plate.

Because of the failure of the culture material and in order to obtain a complete timed series of developmental stages, attached copepodites were taken from host material and placed in individual stender dishes. After these copepodites moulted into the first chalimus (the following stage), the time was noted until the succeeding moult, into the second chalimus. To ascertain the time passed in each stage after the first chalimus, specimens of the previous stage were taken from the host and treated as above. Due to the mortality rate under laboratory conditions, many specimens of each stage had to be collected so that one would pass through the succeeding stage. Because of the inability to get any number of specimens to pass through each stage and due to the necessity of submitting the larvae to laboratory conditions, the time indicated for each stage in Figures 2-7 should be regarded as indicative, not conclusive.

The descriptions of the body, appendages, and processes of all of the developmental stages and the adult is followed by a discussion of the general behavior of the various developmental stages. The graphical figures included in the

text (Figs. 2-7) give the means and ranges of various measurements of the larval forms.

Larval specimens other than nauplii were killed and preserved in 95% ethyl alcohol. Specimens to be dissected were placed in 85% lactic acid to soften and clear them, stained with methyl blue dissolved in 85% lactic acid, and dissected in clear 85% lactic acid.

Drawings of the total animal were made from specimens placed in 85% lactic acid and covered with a 9 mm cover slip. The cover slip was raised slightly above the younger specimens by thin pieces of glass so that the specimen was not distended. A camera lucida and a Bausch and Lomb arc projector were used to make the drawings of the total animal. Drawings of the appendages and processes were made, with the use of a camera lucida, from appendages and processes either in situ on the whole mount or dissected off and mounted in Hoyer's mounting medium. Measurements were made with an ocular micrometer.

The terminology used, with some exceptions which are given in the text, is that used in Lewis (in press). To facilitate the use of the thoracic leg tables, a hypothetical thoracic leg is shown in Figure 1, giving all of the component parts of the armament of the thoracic legs discussed in tabular form in this publication. Further, a table of the hypothetical thoracic leg is given below in Table 1.

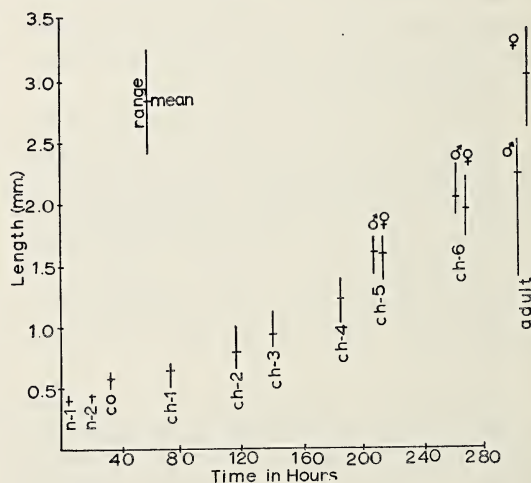


FIG. 2. Greatest length of body, excluding setae, in developmental stages of *L. dissimulatus*. n, Nauplius; co, copepodite; ch, chalimus.

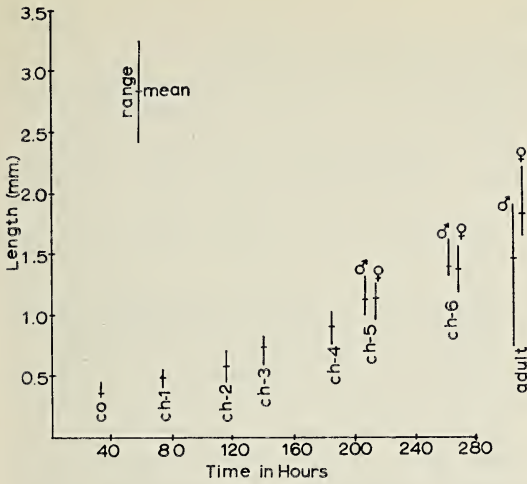


FIG. 3. Greatest length of cephalothorax, including frontal plates, of developmental stages of *L. dissimulatus*. co, Copepodite; ch, chalimus.

DEVELOPMENT AND DESCRIPTION OF LIFE HISTORY STAGES

As the eggs are extruded out of the oviducal opening at the posterior end of the genital segment they are fertilized by sperm from the seminal receptacle (Wilson, 1905:526). Two spermatophores are implanted by the male on the external posterior ventral surface of the female genital segment and open into the two oviducts through the seminal receptacles (Wilson, 1905:527). The disk-shaped fertilized eggs are extruded as a uniseriate chain (Fig. 8a). Each egg is wrapped in a cuticular material, presumably secreted by a cement gland in the genital segment of the female, that remains attached to the female until after the eggs hatch (Fig. 8b). The covering appears to serve as a protective structure for the eggs and developing embryos and as a means of connecting the eggs together in a string.

Because of the flattening of the fertilized eggs, development is difficult to observe. From 13–20 hr (at room temperature, approximately 23 C) after extrusion, a reddish-colored eye spot becomes visible on the yellowish or whitish embryo. From 30 to 40 hr (at room temperature) after extrusion, movement is visible within the egg. As the movement of the embryo increases, the egg expands and finally ruptures. Hatching occurs regularly, the distal egg

hatching first, the proximal last. A lapse of between 2 and 10 min occurs between the hatching of one egg and the hatching of the succeeding one. In almost all cases, the egg chamber ruptures on the inner side of the egg string (i.e., the surface nearest the median longitudinal axis of the female). The first nauplius, by sporadic violent movements of its appendages, works its way out of the egg case and, after a short period of rest in which some swelling occurs, assumes the characteristic jerky, free-swimming habit of the naupliar stages.

Body

The externally unsegmented body of the first nauplius (Fig. 8c) is of a general obovoid shape in both dorsal and lateral aspects. The greatest length is slightly more than twice the greatest width, and the anterior end is broadly curved. The lateral margins of the posterior one-half of the body curve inward regularly to the irregularly-margined posterior end. The posterior end of the body has a slight median projection and two indentations, one on each side, from which the balancers arise. The balancers (Fig. 16k) are unsegmented, slightly curved, rodlike structures that project laterally and have their distal end slightly flattened.

The cuticle of the first nauplius is, in most specimens, slightly larger than the inner body;

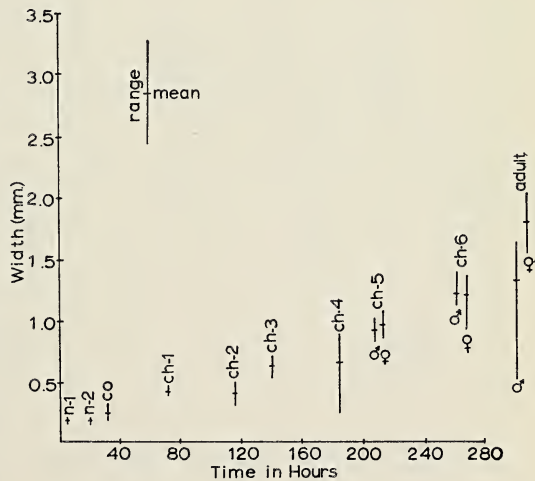


FIG. 4. Greatest width of body, excluding marginal flanges, of developmental stages of *L. dissimulatus*. n, Nauplius; co, copepodite; ch, chalimus.

TABLE 1
ARMATURE OF HYPOTHETICAL THORACIC LEG SHOWN IN FIGURE 1

MARGIN	STERNAL PLATE	PROTOPODITE		EXOPODITE			ENDOPODITE		
		1	2	1	2	3	1	2	3
Outer	f		1rh		1H	2H,1Hm,1Q	c,C	c,1h	c,2p',2P
Inner		1P	f,1p,1s	1H'	c,1P	c,5P	1P'	c,2P	2P

a distinct space is visible between the anterior end of the body and the cuticle. There is indistinct evidence of internal segmentation posteriorly. The general body color in life is light yellow with numerous red and blue pigment spots scattered over the surface. The eyes are visible as two minute, clear, round lenses, one on each side of an irregular, reddish-pigmented region in the anterior portion of the body. The alimentary tract is not visible, neither are the mouth nor the anus. Large globules of material, presumably yolk, are evident, clustered in an indistinctly delimited, oblong mass extending posteriorly from just behind the ocular region.

The first nauplius possesses three sets of appendages (described later), the uniramous antennules, biramous second antennae, and biramous mandibles in this order proceeding posteriorly. All of these appendages possess long,

lightly plumose setae that presumably function as flotation mechanisms and in swimming.

The first naupliar stage lasts for 4½–13 hr with an average of 6½ hr (based on nine hatchings at room temperature, approximately 23 C). After this time the movement of the animal decreases slightly and the cuticle splits longitudinally at the dorsal anterior end. The nauplius then wriggles violently and breaks through the split, freeing itself from the cuticle.

The body of the second nauplius (Fig. 8*d, e*) is similar to that of the first, although the length from the mandibles to the posterior end of the body is greater. The greatest length, excluding the appendages, is almost 2½ times the greatest width. The body is very slightly flattened dorsoventrally in cross section, the anterior end is broadly curved, and the lateral margins are flatly convex. The posterior end of the body is similar to that of the first nauplius although the balancers are slightly larger and arise from two small, circular, platelike processes in the posterior lateral indentations (Fig. 16*l*).

The bodies of older second nauplii have a small space between the anterior end and the cuticle. There is distinct evidence of internal segmentation, similar to the segmentation of the copepodite, visible inside the cuticle of older specimens but not visible on the external surface. The alimentary tract is indistinct and incomplete, visible only as a cluster of yolk globules along the median longitudinal axis just posterior to the ocular region.

The basic structure of the three sets of appendages of the second nauplius is similar to that of the first. The armature, however, is slightly different. This stage lasts for 9½–19 hr with an average of 14½ hr (based on eight hatchings at room temperature, approximately 23 C). Just prior to moulting into the copepodite stage, the movement of the animal be-

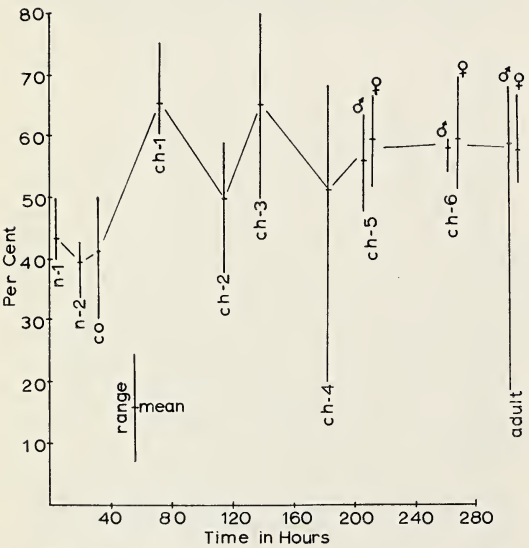


FIG. 5. Greatest width as a per cent of total body length, excluding setae, of developmental stages of *L. dissimulatus*. n, Nauplius; co, copepodite; ch, chalimus.

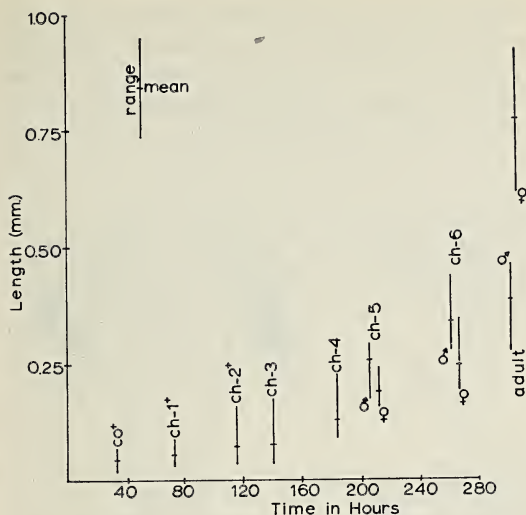


FIG. 6. Greatest length of genital segment of developmental stages of *L. dissimulatus*. co, Copepodite; ch, chalimus; +, measurement includes both genital segment and abdomen (one segment in early stages).

comes sporadic, stopping at times and then becoming vigorous. During one of the vigorous periods of movement a crack appears in the anterior dorsal portion of the cuticle and the copepodite wriggles out in the same manner as in the previous moult.

The change from the second nauplius to the copepodite is the greatest change that occurs in a single moult during development. In one moult the body is divided from an externally unsegmented structure into a cephalothorax consisting of the head, maxilliped-bearing segment, and first pedigerous segment. Further, four free segments are visible posterior to the cephalothorax. The first of these segments bears the second thoracic legs, the second bears a pair of posteriorly directed spines that may be the predecessors of the third thoracic legs, the third free segment is naked but will later give rise to the fourth thoracic legs, and the fourth free segment, to which the caudal rami are attached, will later differentiate into the genital segment and abdomen.

Not only does the body break up from a relatively undifferentiated second nauplius to a copepodite with a composition comparable to that of the adult, but also most of the appendages and processes are now present. Besides the

antennules, second antennae, and mandibles that were present on the first and second nauplius, the postoral processes, maxillae, maxillipeds, and first two pairs of thoracic legs have been added and the caudal rami are now present.

The general shape of the copepodite body (Fig. 8f) is ovoid in both dorsal and lateral aspects. The greatest width, that of the cephalothorax, is less than one-half the greatest length (Fig. 5). The anterior cephalothoracic margin is sharply convex and the lateral margins are flatly convex. A pair of V-shaped indentations, or sinuses, are visible in the posterior lateral margin of the cephalothorax. These posterior sinuses are found at the junction of the posterior surfaces of the median and lateral cephalothoracic areas and suggest that the lateral areas are distinct from the median and are an outgrowth of the cephalon. This is further indicated by the longitudinal cephalothoracic grooves which, in the copepodite, run anteriorly for a very short distance from the apex of the posterior sinuses. The median cephalothoracic area does not extend past the posterior lateral area and its posterior margin is irregular. The eyes are distinct and similar to those of the naupliar stages.

The free second pedigerous segment is wider than long, its greatest width being 1.3 times the length. Both the anterior and posterior margins

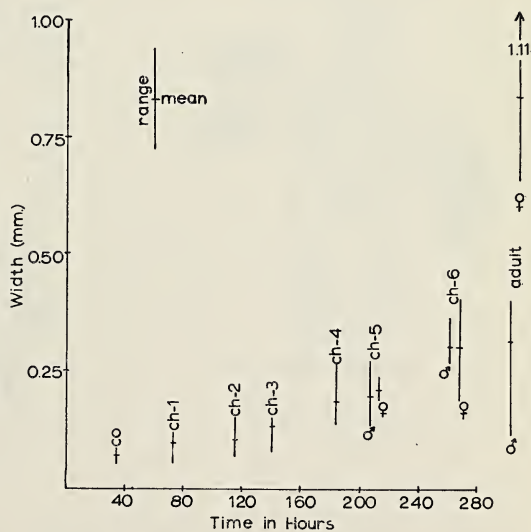


FIG. 7. Greatest width of genital segment of developmental stages of *L. dissimulatus*. co, Copepodite; ch, chalimus.

are distinct, the anterior being irregularly convex and the posterior irregularly concave; the lateral margins are broadly convex. The free third pedigerous segment is approximately two-thirds the width of the second and is slightly

wider than long. The lateral margins of the segment are broadly convex in younger specimens, straight in older; the width of the posterior end of the segment is slightly greater than that of the anterior in older specimens but equal to or

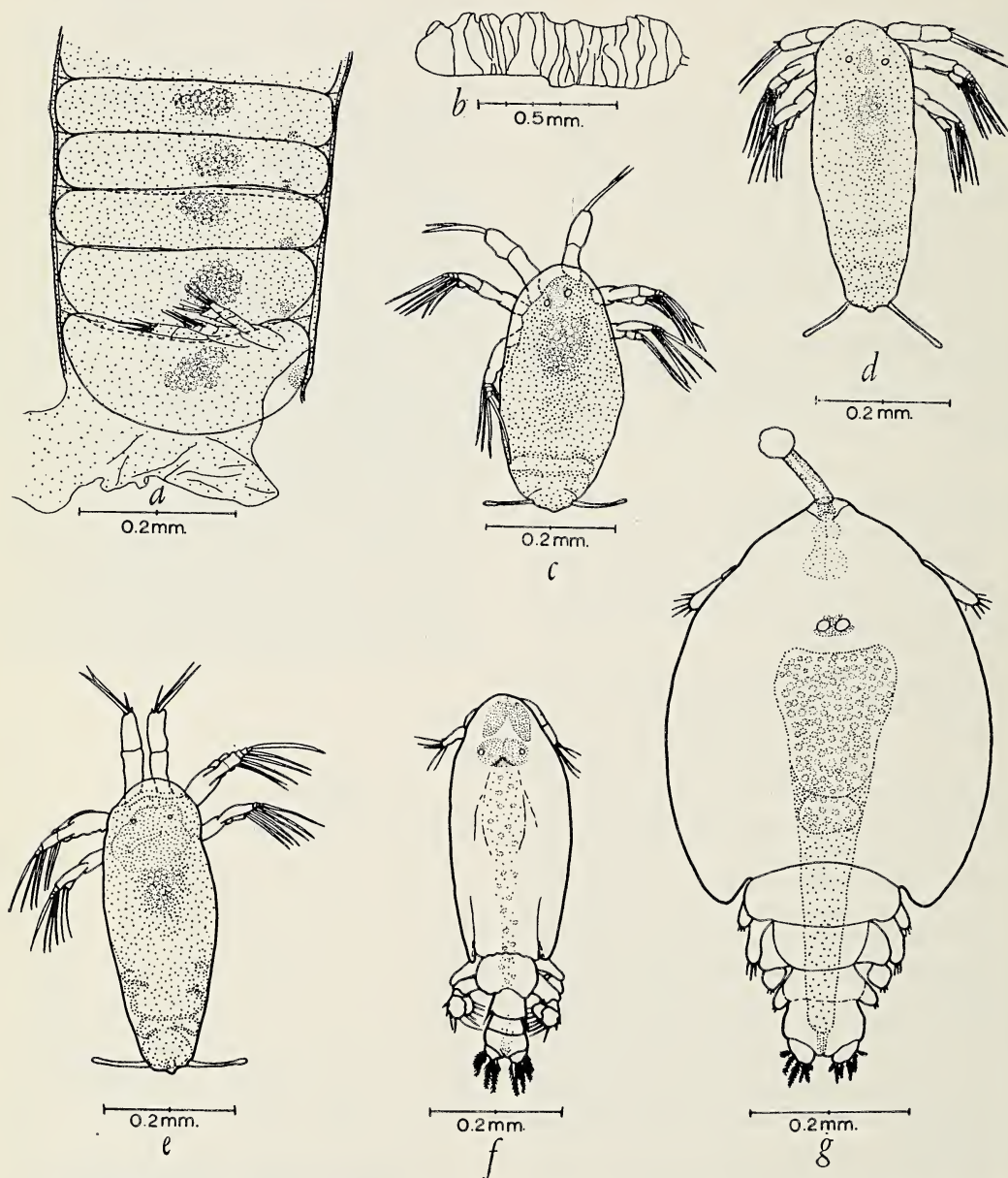


FIG. 8. Egg string of *L. dissimulatus* and body of developmental stages from nauplius to first chalimus. *a*, Posterior end of ruptured egg string, showing first nauplius just emerging; *b*, empty egg string after hatching; *c*, dorsal view of first nauplius; *d*, dorsal view of early second nauplius; *e*, dorsal view of late second nauplius; *f*, dorsal view of copepodite; *g*, dorsal view of first chalimus. Stippled circles, yolk material.

slightly less than the width of the anterior end in younger specimens. The third pedigerous segment bears a single naked, spinelike process projecting from each of the posterior lateral corners (Fig. 12a). The relationship of this process to the future third thoracic leg is unknown although Heegaard (1947:63, fig. 8) figures a pair of lobate appendages in the same region as the spines and indicates that they become the third thoracic legs of *Caligus curtus*. The free fourth pedigerous segment is short, its greatest width being almost 3 times its length. The anterior margin is concave, the posterior convex. There is no indication of the fourth thoracic legs.

The free fourth segment, the future genital segment and abdomen, is slightly shorter than the combined lengths of the third and fourth pedigerous segments, and the width is slightly greater than the length. The lateral margins are flatly convex, and the lateral posterior margins are concave, forming the attachment surface, and possibly an articulation surface, for the caudal rami. The posterior medial margin of the segment is bilobed, and the anal region is evident as a minute, V-shaped depression between the lobes.

The copepodite possesses a spikelike rostrum on the anterior end of the cephalothorax (Fig. 13a). The frontal organ is now visible, although rather indistinctly, and is represented by two large ovoid bodies at the anterior end of the cephalothorax that are connected to the rostrum by a slender, tubelike process. The alimentary tract is visible as two convex lines extending from just behind the eyes posteriorly for approximately one-third the length of the cephalothorax. The tract is visible posterior to the two convex lines only as a slender mass of yolk globules along the median longitudinal axis and extending posteriorly to the free third pedigerous segment. There does not appear to be an oral opening.

The length of time spent in the copepodite stage is not known due to the inability of getting a copepodite to attach to a substrate and moult into the first chalimus in the laboratory. In order to determine the method of attachment, observations were made on specimens of copepodites attached to host material collected in the field. The copepodite attaches to the host by

means of the second antennae, secretes a frontal filament, and then after a short period of time moults into the first chalimus. This process is described in detail in the portion of the paper devoted to the general behavior of the developmental stages. The only visible difference between the free-swimming and attached copepodites is the slightly larger frontal organ in the attached forms. All of the appendages and processes and the general body structure are identical. Heegaard (1947:53–65), however, describes two copepodite stages for *Caligus curtus*, the first copepodite moulting into the second shortly after the host is found. In addition he describes a "pupal stage" that is passed within the loosened but unshed second copepodite cuticle. Neither the second copepodite stage nor the pupal stage were found in *Lepeophtheirus dissimulatus*.

The change from the copepodite to the adult is gradual for the most part. There are exceptions to this in some of the appendages such as the first and second thoracic legs but, in general, the transition occurs in a step-by-step manner through the six chalimus stages which are found between the copepodite and the adult.

The first chalimus (Fig. 8g), attached to the host by the frontal filament, is dorsoventrally flattened. The body is ovoid in a dorsal view and the greatest length, including the frontal region but not the frontal filament, is approximately 1.2 times the greatest width. The cephalothorax consists of the cephalon, maxilliped-bearing segment, and first pedigerous segment as in the copepodite. The second, third, and fourth pedigerous segments, in addition to the single segment that will later form the genital segment and abdomen, are free. The anterior margin of the cephalothorax is broadly curved except for an irregular median swelling in the region of the frontal filament. The lateral cephalothoracic margins flare slightly anteriorly, just posterior to the antennule base, and then curve flatly posteriorly. The posterior sinuses are distinct but are formed of the anterior lateral margin of the second pedigerous segment and the inner margin of the posterior lateral cephalothoracic area, not the outer margin of the median cephalothoracic area and the inner margin of the posterior lateral cephalothoracic area as in the copepodite. The median margin of the thoracic area is flatly

convex and extends between the apices of the posterior sinuses. The eyes are similar to those of the preceding stages and are situated in the anterior one-third of the cephalothorax. Cephalothoracic grooves are indistinctly present or absent although some irregular dorsal grooves are usually present in the anterior part of the body.

The free second pedigerous segment is much wider than in the copepodite, being more than 3 times as wide as long. The lateral margins are smoothly convex, the posterior margin flatly convex. The free third pedigerous segment is approximately $2\frac{1}{2}$ times wider than long, the posterior end is narrower than the anterior, the lateral margins are flatly convex, and the posterior margin is flat. The third thoracic legs are now present, the spinelike processes of the copepodite being absent. The fourth pedigerous segment is shorter than the third, the width is slightly more than twice the length, and the posterior region projects laterally slightly at the junction of the now present fourth thoracic legs. The posterior margin of the segment is indistinct and irregular.

The combined genital segment and abdomen (Fig. 12*b*), that form the fourth free segment, are similar in both shape and measurements to that of the copepodite.

The frontal region (Fig. 13*b*) is slightly irregular; the rostrum of the copepodite is absent. The frontal organ consists of two lobate processes at the base of the frontal filament, an additional two lobate processes attached to the posterior surface of the first two, and an irregular indistinct area posterior to the second set of processes. The frontal region is not distinctly separated from the cephalothorax although an indistinct groove is present on the ventral surface, extending from the lateral margin, in the region of the antennules, posteriorly and then across the ventral surface.

The first chalimus stage lasts for approximately 40 hr (based on two specimens kept at room temperature, approximately 23 C) at which time the specimens moult into the more elongate second chalimus.

The general shape of the second chalimus (Fig. 9*a, b*) is similar to that of the first chalimus. The cephalothorax now includes the second pedigerous segment in addition to the first.

Late in this stage, however, the division between the cephalothorax and the third pedigerous segment becomes indistinct (Fig. 9*b*). The greatest length of the cephalothorax, including the frontal region, is approximately $1\frac{1}{2}$ times the greatest width, considerably longer than the cephalothorax of the first chalimus. The increase in length is presumably due to the inclusion of the second pedigerous segment in the cephalothorax. The anterior margin of the cephalothorax is broadly rounded except for the median protrusion of the frontal filament; laterally, the margin turns posteriorly sharply, then flares slightly to the lateral cephalothoracic margins. The lateral margins are wavy in some specimens and smooth in others although the entire margin is generally convex. The posterior cephalothoracic margin is four-lobed in the early second chalimus, with two large lobes in the lateral region of each side. In older specimens of this stage, in which the division between the cephalothorax and the third pedigerous segment is indistinct, the inner two lobes are not visible and the median cephalothoracic area, the third pedigerous segment, projects well past the lateral areas. The posterior sinuses are distinct as two small, V-shaped depressions between the two lobes in the younger specimens and between the inner margin of the lateral areas and the outer margin of the median cephalothoracic area in the older specimens. Thus far then, the posterior sinuses appear to be due to the unequal growth of the lateral and medial regions of the cephalothorax. The dorsal cephalothoracic grooves are indistinct, consisting of a single, very short groove extending anteriorly from the apex of each of the two posterior sinuses.

The third pedigerous segment, free in the early second chalimus, tapers evenly from the junction with the second pedigerous segment to the junction with the free fourth pedigerous segment. The greatest length of the segment is approximately four-fifths the greatest width and about one-fifth that of the cephalothorax. The free fourth pedigerous segment flares outward from the junction of the third to the attachment of the fourth legs, at the posterior end of the segment. The greatest width of the segment is approximately 1.6 times the greatest length, slightly more than one-half that of the third pedigerous segment. The division between the

third and fourth pedigerous segments is distinct, between the fourth and the genital-abdominal segment also distinct although sometimes faint in younger specimens.

The combined genital segment and abdomen (Fig. 12*c*) is slightly shorter than the third

pedigerous segment, and its greatest width is slightly more than its length. The lateral margins are flatly convex; the lateral posterior margins are flat or slightly concave and form the place of attachment for the caudal rami. The anal laminae are visible as two knoblike projec-

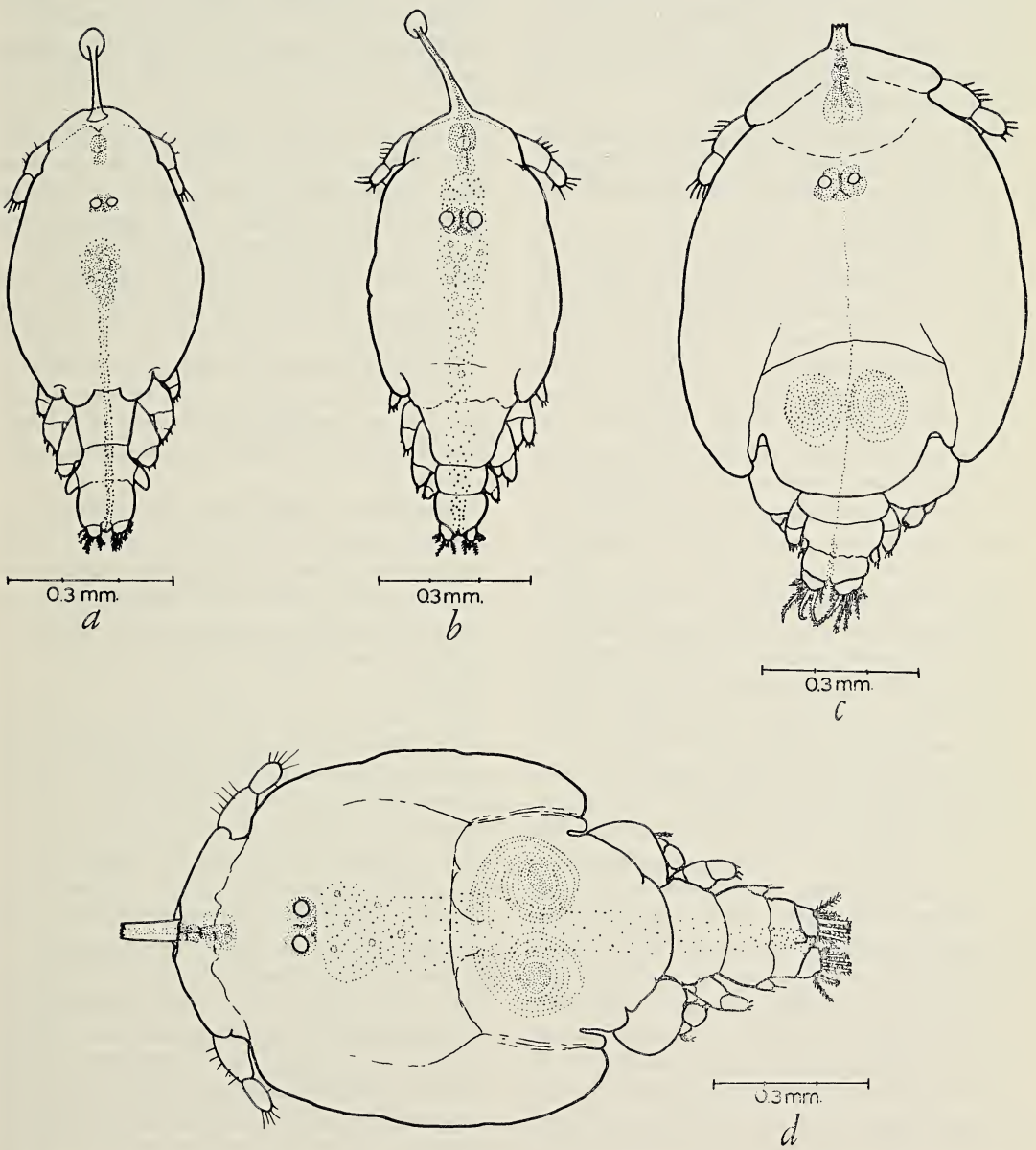


FIG. 9. Body of second, third, and fourth chalmus developmental stages of *L. dissimulatus*. *a*, Dorsal view of early second chalmus; *b*, dorsal view of late second chalmus; *c*, dorsal view of third chalmus; *d*, dorsal view of fourth chalmus. Stippled circles, yolk material.

tions and form the middle of the posterior surface of the segment.

The frontal organ of the second chalimus (Fig. 13c) is similar to that of the first chalimus although more distinct. The lobes at the proximal end of the frontal filament are contiguous along the median longitudinal axis of the body, forming a single ovoid structure; the lobes posterior to the first set are slightly smaller than in the preceding stage. The alimentary tract now appears complete although the anterior end is still filled with yolk granules.

The 10 specimens maintained successfully in the laboratory, at room temperature (approximately 23 C), remained in the second chalimus for about 42 hr.

The third chalimus (Fig. 9c) is somewhat wider than the second. The greatest length, including the frontal region but not the frontal filament, is approximately 1.3 times the greatest width. The cephalothorax now includes the first three pedigerous segments, the condition occurring in the adult. The fourth pedigerous segment is free and forms the connection between the cephalothorax and the now indistinctly differentiated genital segment and abdomen. The frontal region (Fig. 13d) is still indistinctly separated from the cephalothorax. The anterior margin of the frontal region is flatly tapered from the projection of the frontal filament laterally. The lateral portions of the frontal margin are evenly rounded and join the lateral margins of the cephalothorax at a slight indentation marking the origin of the groove incompletely dividing the frontal region from the cephalothorax. The lateral margins of the cephalothorax are smoothly convex, the posterior lateral corners rounded. The posterior sinuses are distinct and U-shaped; the lateral margins of the median thoracic area are continuous with the inner margins of the sinuses. The median thoracic area extends posteriorly past the posterior extensions of the lateral areas. The reddish-pigmented regions of the eyes encircle all but the outer portion of the lenses, a large increase in the amount of pigmented material over the preceding stages. The cephalothoracic grooves are distinct, the major ones forming an H. The longitudinal grooves of the H extend anteriorly and curve medially from their origin just lateral to the apices of the posterior sinuses. The two

grooves are connected by an anteriorly curving cross groove in their anterior region. Other indistinct grooves are present in the anterior region of the cephalothorax.

The free fourth pedigerous segment is short and partially covered by the posterior portion of the median cephalothoracic area. The greatest length of the segment is approximately one-half the greatest width. The lateral margins are convex; the posterior margin is distinct, completely separating the segment from the genital segment.

The genital segment (Fig. 12d) is short, the length slightly more than one-half the greatest width, approximately equal to the length of the fourth pedigerous segment. The lateral margins are convex anteriorly and indented posteriorly. The posterior margin is light but distinct, and the abdomen is now considered distinct from the genital segment. A pair of one-segmented dactyliform processes, the fifth legs, are visible extending posteriorly from the posterior lateral surface of the genital segment. The distal end of the fifth leg is rounded and bears two plumose setules.

The abdomen (Fig. 12d) is short, the greatest length slightly less than that of the genital segment, the greatest width approximately $2\frac{1}{2}$ times the length. The lateral margins are convex and the posterior margins curve medially to the bilobed anal region, composed of the anal laminae.

The frontal organ (Fig. 13d) is slightly smaller than that of the second chalimus and consists of four parts. The first part is formed of two oval bodies at the base of the frontal filament, one on either side of the median longitudinal axis, that are contiguous along their inner margins. A somewhat larger circular body is present, attached to the posterior surface of the two anteriormost bodies. An elongate, bifurcate body is attached to the posterior surface of the circular body; both distally rounded parts of the bifurcation extend posteriorly and slightly laterally into a larger semirectangular fourth part. The change in the shape of the organ from the preceding chalimus may be due to a shrinking of the structure, the anterior two parts being formed from the single ovoid structure present on the second chalimus; the semirectangular fourth part can not be traced to any definite

area in the frontal organ of the preceding stage. Yolk material is still visible in the alimentary tract and is concentrated in an enlarged area just posterior to the ocular region.

Eight specimens of the third chalimus lasted for approximately 33 hr at room temperature (approximately 23 C) at which time they moulted into the more elongate fourth chalimus.

The elongate condition of the fourth chalimus indicates a cyclic condition in the growth of the first four chalimus stages (Fig. 5). The average greatest length of the first chalimus (11 specimens), excluding setae, is 1.54 times the greatest width, of the second chalimus (45 specimens) is 2.04 times the width, of the third chalimus (25 specimens) is 1.54 times the width, and of the fourth chalimus (74 specimens) is 1.95 times the width. This cyclic tendency, from stubby to elongate to stubby to elongate, in the relationship between the greatest length and greatest width in the first four chalimus stages can not be explained by the growth of any single structure or body part. There appears to be a cyclic growth tendency in several body parts. For example, the cephalothorax length as a per cent of the total length is 79.1, 74.3, 79.5, and 73.6 for the first four chalimus stages respectively; the maximum width of the genital-abdominal segment as a per cent of the maximum length of the segment is 186.0, 153.6, 180.0, and 153.8 (genital segment only for this last measurement) for the first four stages respectively. Certainly, the inclusion of the second pedigerous segment into the cephalothorax affected the length of the cephalothorax as a per cent of the total length measurements in the second chalimus but the fact that the third pedigerous segment was included in the cephalothorax in the third chalimus did not appear to affect the trend in that stage.

The cephalothorax of the fourth chalimus (Fig. 9d) is ovoid in outline as in the preceding chalimus stages. The greatest length of the cephalothorax, including the frontal region but not the frontal filament, is slightly more than 1.3 times the greatest width. The frontal region and frontal plates are now distinct and the division of the region from the cephalothorax is complete. The division between the frontal region and the cephalothorax forms an irregular groove curving anteriorly from its origin on the

anterior lateral margin. The anterior margin of the frontal region is broadly curved, the anterior lateral surfaces forming laterally projecting lobes, the posterior lateral margin connecting these lobes to the lateral margins of the cephalothorax. The lateral cephalothoracic margins are generally convex, although wavy; the posterior lateral corners are rounded. The lateral posterior margins, outside the posterior sinuses, are bilobed, consisting of the broadly rounded posterior lateral extensions of the lateral regions and the narrow, lobate lateral surface of the median thoracic area. The posterior sinuses are distinct and slender, generally V-shaped although sometimes U-shaped. The median thoracic area extends posteriorly well past the posterior extensions of the lateral regions and is irregularly tapered to the slightly rounded posterior margin. The lateral margins of the median thoracic area are continuous with the inner margins of the posterior sinuses. The major cephalothoracic grooves, as in the preceding stage, form an H. The anterior legs of the H, however, curve laterally from the junction with the cross groove anteriorly to their termination lateral and just posterior to the eyes. The lateral strengthening regions of the adult are not yet visible.

The free fourth pedigerous segment is short, its greatest length approximately two-thirds its width. The anterior end of the segment is overlapped by the posterior extension of the median thoracic area of the cephalothorax. The lateral margins taper both anteriorly and posteriorly from the widest point, in the middle of the segment, at the junction of the fourth thoracic legs. The posterior margin is distinct, forming a flatly convex groove.

The genital segment (Fig. 12e) is slightly shorter than the fourth pedigerous segment; its greatest length, excluding the slightly projecting fifth legs, is approximately two-thirds its width. The widest point is in the posterior medial region of the segment. The anterior lateral margins curve convexly, the posterior lateral margins concavely. The fifth legs project as dactyli-form processes from the concave posterior lateral margins and extend slightly past the posterior end of the segment. The legs are tipped by two small plumose setae. The posterior margin of the segment is distinct although irregular.

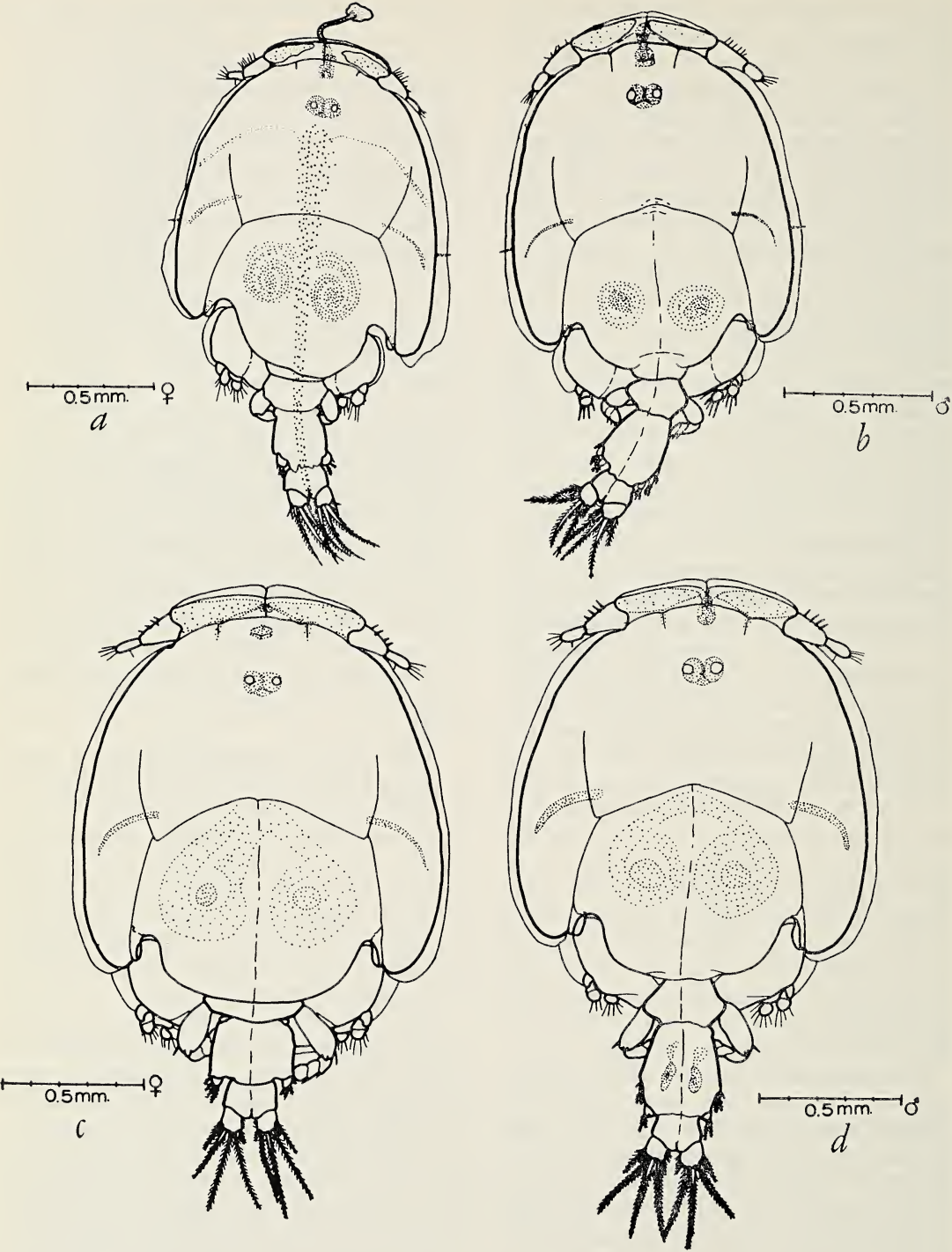


FIG. 10. Body of fifth and sixth chalmus developmental stages of *L. dissimulatus*. *a*, Dorsal view of attached female fifth chalmus; *b*, dorsal view of free-moving male fifth chalmus; *c*, dorsal view of free-moving female sixth chalmus; *d*, dorsal view of free-moving male sixth chalmus.

The abdomen (Fig. 12e) is slightly more than one-half the length of the genital segment; its greatest width is approximately twice the greatest length. The lateral margins are flatly convex or straight; the lateral posterior margins are slightly concave and taper to the median, bilobed anal region.

The bifurcate third part of the frontal organ (Fig. 13e) now extends to the posterior end of the smaller semirectangular fourth part. Both parts of the bifurcation are club-shaped and do not extend laterally as in the third chalimus. The alimentary tract is the same as that of the preceding stage although there is not as much yolk material.

Three specimens of the fourth chalimus lasted for about 36 hr under laboratory conditions (temperature approximately 23 C.) before they moulted into the fifth chalimus.

The fifth chalimus (Fig. 10a, b) is found both attached and free on the host although more frequently attached. With the exception of a few structures such as the genital segment and some of the appendages, the somewhat flabby condition of the body and appendages characteristic of earlier chalimus larvae is absent and the stage is quite similar to the adult. The greatest length of the cephalothorax, including the frontal region, is approximately 1.3 times its greatest width, excluding the now present marginal flanges. The frontal plates form most of the frontal region and a narrow, membranous flange projects from its broadly curved anterior margin. The lateral frontal region surfaces project slightly, the posterior lateral margins connecting the lobate projecting portions to the lateral margins of the cephalothorax. The division between the cephalothorax and the frontal region is a distinct three-lobed groove, the median lobe of which is approximately twice the length of the lateral lobes. The lateral margins of the cephalothorax are broadly curved, with distinct marginal flanges extending from the junction of the frontal region posteriorly around the posterior extensions of the lateral regions to the beginning of the posterior sinuses. The lateral posterior margins, outside the posterior sinuses, are bilobed and consist of the rounded posterior extensions of the lateral regions and the sharply rounded lateral surface of the median thoracic area. The posterior sinuses are distinct and U-

shaped. The median thoracic area extends posteriorly well past the posterior extensions of the lateral regions; its posterior margin is broadly rounded but possesses a small, median protrusion that forms the junction of the free fourth pedigerous segment in the now discernible male but which is absent in the female. The lateral margins of the protruding median thoracic area are continuous with the inner margins of the posterior sinuses. The major cephalothoracic grooves are similar to those of the preceding chalimus but appear more definite and not quite as irregular. Two heavily sclerotized regions, the lateral strengthening regions, are visible as posterior laterally curved, rodlike structures in the cephalothorax, originating just anterior and slightly medial to the junction of the longitudinal legs of the cephalothoracic grooves and extending to the region of the lateral margins.

The free fourth pedigerous segment is short; its greatest length is approximately one-half its greatest width. The posterior portion of the median thoracic area of the cephalothorax overlaps the anterior end of the segment slightly in the female but not in the male. The lateral margins are convex, the middle of the segment being the broadest region and slightly overlapping the proximal end of the fourth thoracic legs. The posterior margin is distinct although slightly irregular.

Because of the presence of the sixth thoracic legs on the male of this stage, the sexes can now be differentiated, as the female does not possess this appendage pair. As will be discussed later, the second antennae can not be used in differentiating the sexes of any of the chalimus stages of *L. dissimulatus*. The presence or absence of the sixth legs is the best method so far found by which the sexes can be told apart in both the fifth and sixth chalimus stages.

The genital segment of the female (Fig. 12g) is as wide as long; the lateral margins are flatly or broadly convex. The anterior end possesses two lateral, rounded protuberances that are distinct in a dorsal view but indistinct in a ventral view. The posterior lateral margins are indented, the lobate fifth legs arising from the ventral surface and projecting posteriorly. The fifth leg does not project past the posterior end of the genital segment as in the preceding stage. Four plumose setae, an additional two setae over the

last stage, are spaced along the outer margin of the fifth leg. The posterior margin of the female genital segment is broadly rounded in some specimens and irregular in others.

The male genital segment (Fig. 12f) is similar to that of the female although slightly longer; the lateral margins are, however, not indented in the dorsal view. Both the fifth and sixth legs arise from the posterior ventral lateral surface, adjacent to each other. Further, both legs are lobate, the sixth extending slightly past the division between the genital segment and abdomen. The fifth leg possesses one plumose setule on the outer base of the leg and two plumose setae on the distal end; the sixth leg is tipped by two plumose setules.

The abdomen (Fig. 12f, g) is bell-shaped and short; its greatest length is one-half that of the genital segment in the males, slightly longer in the females, and the greatest width is approximately $1\frac{1}{4}$ times the length. The posterior region of the single abdominal segment is broader than the anterior, the lateral margins are convex, and the lateral posterior margins are concavely tapered to the bilobed anal region.

The frontal organ (Fig. 13f) is similar to that of the preceding stage although the component parts are less distinct. The attachment filament, if present, arises from a circular indentation on the anterior ventral surface just anterior to the frontal organ. In unattached forms this circular indentation forms a scar which is the only evidence of the attachment filament. The yolk material that was present in the fourth chalimus now appears to be completely absent.

Only two specimens survived from the moult into the fifth chalimus to the moult into the sixth. Both of these specimens spent approximately 24 hr in the fifth chalimus stage under laboratory conditions (temperature approximately 23 C).

The sixth chalimus stage (Fig. 10c, d) is the last larval stage. Specimens in this stage of development were found both attached and free although, in contrast to the fifth chalimus, more frequently free. The greatest length of the cephalothorax, including the frontal region, is approximately 1.2 times the greatest width, excluding the marginal flanges. The frontal region is similar to that of the fifth chalimus. The lateral margins of the cephalothorax are broadly

curved and are fringed with a distinct marginal flange. The posterior lateral corners of the cephalothorax are broadly rounded; the lateral posterior margins, outside the posterior sinuses, are bilobed, as in the preceding two stages, and consist of the rounded posterior extensions of the lateral regions and the sharply rounded lateral posterior surface of the median thoracic area. The posterior sinuses are distinct and U-shaped. The median thoracic area extends posteriorly slightly past the posterior extensions of the lateral areas. The posterior margin of the extension is broadly rounded in the female but has a flat median protrusion in the male. The lateral margins of the extended median thoracic area are continuous with the inner margins of the posterior sinuses. The major cephalothoracic grooves are similar to those of the preceding chalimus stage. Minor cephalothoracic grooves are visible on some specimens and, when present, extend posteriorly from the division between the frontal region and the cephalothorax. The lateral strengthening regions are proportionately larger than in the fifth chalimus but are similar in general shape and position.

The free fourth pedigerous segment is short, its length approximately one-half the width. The anterior end is covered by the posterior end of the median thoracic area of the cephalothorax in the female but not in the male. The middle of the segment protrudes laterally, the fourth thoracic legs being attached to the distal end of the protrusion; the segment tapers from the protrusion to the narrower anterior and posterior ends. The division between the fourth pedigerous segment and the genital segment is distinct although slightly irregular.

The genital segment of the female (Fig. 12i) is slightly longer than wide, its greatest width being approximately four-fifths of the length. The lateral margins are broadly convex, the anterior lateral surface forming an irregular, node-like formation at the junction with the fourth pedigerous segment. The fifth legs arise from the lateral posterior ventral surface but do not extend to the posterior end of the segment; these structures are lobate in outline and possess three plumose setae along their outer margin and one on the distal surface. The seta on the distal surface possesses a minute swelling on the proximal outer margin (Fig. 12j) which is absent in

both the fifth chalimus and the adult but which was present on all of the female sixth chalimus specimens examined.

The genital segment of the male sixth chalimus (Fig. 12*b*) is longer than that of the female; the greatest width is approximately three-fourths the greatest length. The lateral margins are flatly convex, angled slightly from a swelling on the anterior lateral corner, comparable to the nodelike formation on the female, to the widest point in the region of the fifth legs. The posterior region of the segment curves medially from the region of the fifth legs to the abdomen. Both the fifth and sixth legs are lobate, the fifth approximately one-half the length of the sixth. The fifth legs project from the ventral lateral surface of the posterior one-half of the segment and possess a single plumose seta on the anterior end of the outer margin and three plumose setae on the distal surface, an increase of one seta from the fifth chalimus. The sixth legs project from the ventral surface just inside and posterior to the fifth legs and extend posteriorly to the posterior end of the segment. A single plumose seta, absent in the preceding chalimus, is present on the distal one-half of the outer margin of the sixth legs and two plumose setae are present on the distal surface.

The one-segmented abdomen of both sexes (Fig. 12*b, i*) is short, approximately one-third the length of the male genital segment; the length is exceeded somewhat by the width. The anterior end is slightly narrower than the posterior, the outer margin angled slightly from the anterior end to the middle of the segment. The posterior surface tapers from the middle of the segment to the bilobed anal region at the posterior extremity.

The frontal organ (Fig. 13*g*) appears to have degenerated from the previous stage and now consists of two oval bodies contiguous on the median longitudinal axis of the body just posterior to the division between the frontal region and the cephalothorax. These two bodies are connected to the frontal filament in attached forms or to the circular depression in unattached forms by a slender, rod-shaped structure. The digestive tract is the same as that of the preceding stage.

Only one specimen survived from the moult into the sixth chalimus to the moult into the

adult. The time spent by this single specimen in the sixth chalimus was somewhere between 24 and 30 hr at a temperature of approximately 23 C.

After moulting from the sixth chalimus to the adult, the last moult in the life history, all of the appendages and processes remain unchanged. As seen in Figures 2–7, pertaining to the growth of *L. dissimulatus*, the maximum size of the male is almost completely attained by the sixth chalimus stage while that of the female not until the animal is well into the adult stage. Inasmuch as copulation takes place shortly after the terminal moult, the male would be more likely to be near its maximum size in the last larval stage. During the reproductive portion of the female's life, eggs are stored in the genital segment before they are extruded, causing this segment to swell considerably. As the female does not start to ovulate until some time after fertilization, the significant increase in size after the sixth chalimus is due, to a considerable extent, to the enlarged genital segment as is indicated in Figures 6 and 7. The presence of eggs in the genital segment also pushes the fifth legs laterally and, in some instances, obscures them in a dorsal view of the animal.

The cephalothorax of the adult female and male (Fig. 11*a, b*) is ovoid; the frontal region is distinct, separated from the cephalothorax by a trilobed groove. The lateral margins of the cephalothorax are convex and possess a distinct membranous flange. The posterior sinuses are distinct and of a shallow V-shape. The median thoracic region extends posteriorly slightly past the posterior extension of the lateral regions, forming the junction of the cephalothorax and the fourth pedigerous segment. The major cephalothoracic grooves are similar to those of the sixth chalimus; two minor grooves also extend posteriorly, for a short distance, from the junctions of the lateral and median lobes of the trilobed groove separating the frontal region from the cephalothorax. The rodlike strengthening regions are more heavily sclerotized than those of the sixth chalimus but are similar in shape and are in the same position.

The fourth pedigerous segment of the female and male is short; the lateral regions are drawn out at the fourth leg as in the preceding stage. The terminal portions of the lateral ex-

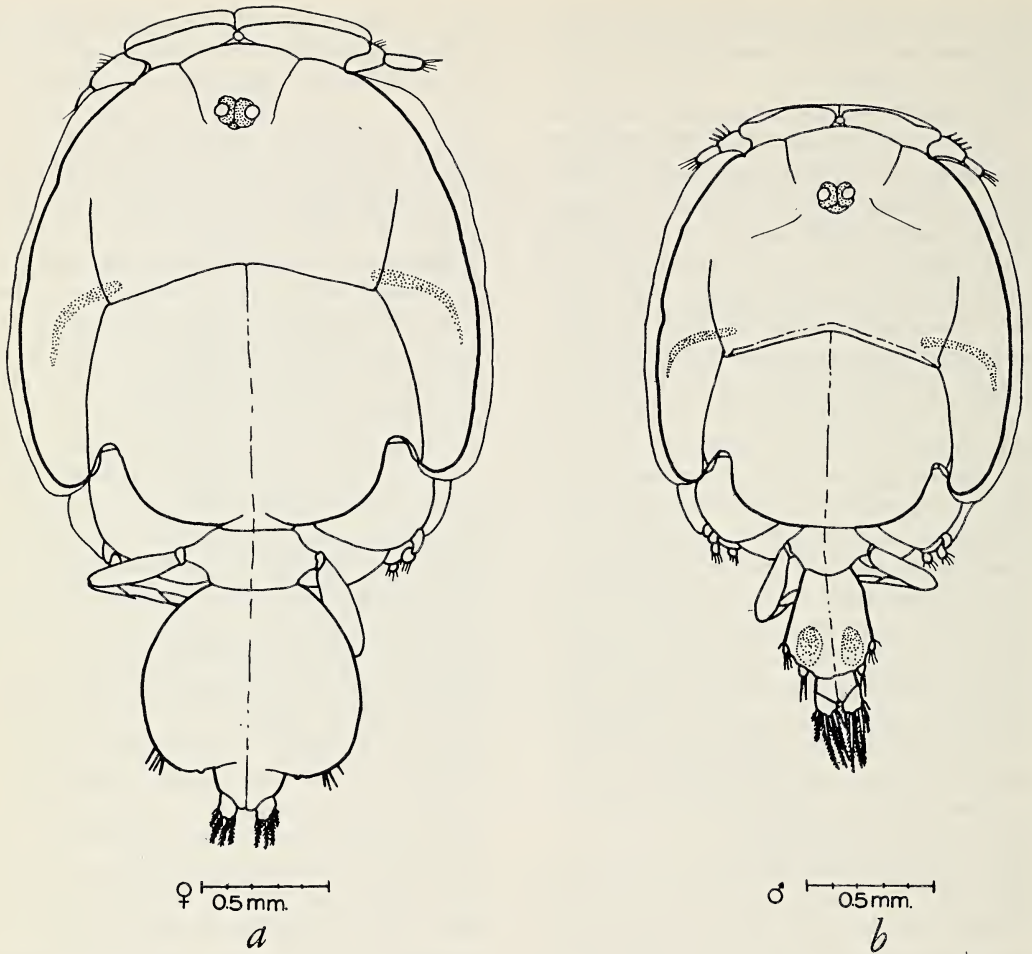


FIG. 11. Body of adult *L. dissimulatus*. *a*, Dorsal view of adult female; *b*, dorsal view of adult male.

tensions are cup-shaped and form socket-like attachments for the fourth legs. The division between the fourth pedigerous segment and the genital segment is distinct and curved convexly.

The shape of the female genital segment (Fig. 12*l*) is variable, dependent upon the number of eggs present in the segment. The segment is flaccid and ovoid in females that have recently extruded egg strings, and is almost circular in females whose genital segment is packed with eggs. Two small knoblike protrusions are present on the posterior margin lateral to the junction of the abdomen; these knobs are characteristic for the female of this species but are not present until the adult stage. The general shape of the fifth legs is similar to that of the

sixth chalimus although the proximal seta of the three plumose setae present on the lateral surface of the leg of the preceding stage now arises from the surface of the genital segment, just lateral to the base of the fifth leg. The movement of this seta may be due to the swelling of the genital segment.

The genital segment of the male (Fig. 12*k*) is ovoid, the width slightly more than three-fourths the length. The shape of this segment and of both the fifth and sixth legs is very similar to that of the sixth chalimus male. The armature of the legs of both stages is identical.

The abdomen of the adult female and male is slightly longer than that of the sixth chalimus (0.12 mm average for 15 sixth chalimus speci-

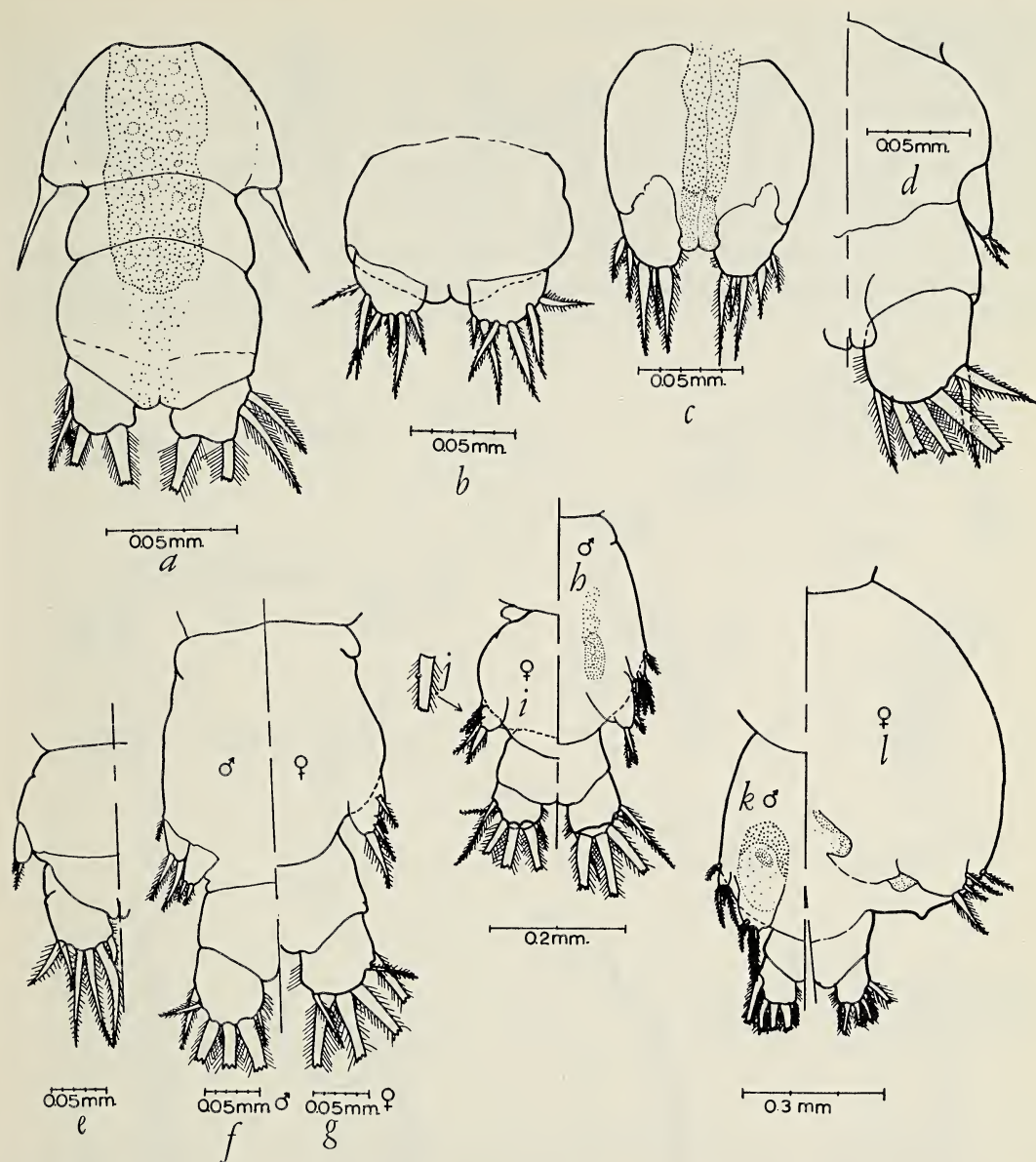


FIG. 12. Genital segment, abdomen, and caudal rami of developmental stages of *L. dissimulatus*. *a*, Copepodite, ventral view showing third and fourth pedigerous segments, genital-abdominal segment and caudal rami; *b*, first chalimus, ventral view of genital-abdominal segment and caudal rami; *c*, second chalimus, ventral view of genital-abdominal segment and caudal rami; *d*, third chalimus, ventral view of genital and abdominal segments, fifth leg and caudal rami; *e*, fourth chalimus, ventral view of genital and abdominal segments, fifth legs and caudal rami; *f*, male fifth chalimus, ventral view of genital and abdominal segments, fifth and sixth legs and caudal rami; *g*, female fifth chalimus, ventral view of genital and abdominal segments, fifth legs and caudal rami; *h*, male sixth chalimus, ventral view showing genital and abdominal segments, beginning of internal spermatophore, fifth and sixth legs and caudal ramus; *i*, female sixth chalimus, ventral view showing genital and abdominal segments, fifth legs and caudal ramus; *j*, enlarged distal seta of female fifth leg showing node on outer proximal surface; *k*, adult male, ventral view of genital and abdominal segments, fifth and sixth legs and caudal ramus; *l*, adult female, ventral view of genital and abdominal segments, fifth legs and caudal ramus.

mens, 0.14 mm average for 30 adult specimens). The general shape, however, is the same.

The frontal organ in the adult (Fig. 13*b*) is greatly reduced, being visible only as a small opaque area on the median longitudinal axis of the body just posterior to the groove dividing the frontal region from the cephalothorax. The attachment filament is completely absent, the only indication of its previous presence being the circular scar mentioned with reference to unattached specimens of the sixth chalimus.

Antennule

Throughout development, from the nauplius to the adult, the antennule is two-segmented. The changes that occur in this appendage are changes in the general shape and relative size of the segments in addition to changes in the armature.

The antennule of the first nauplius (Fig. 14*a*) is uniramous and is attached to the anterior ventral lateral surface of the body. The lateral

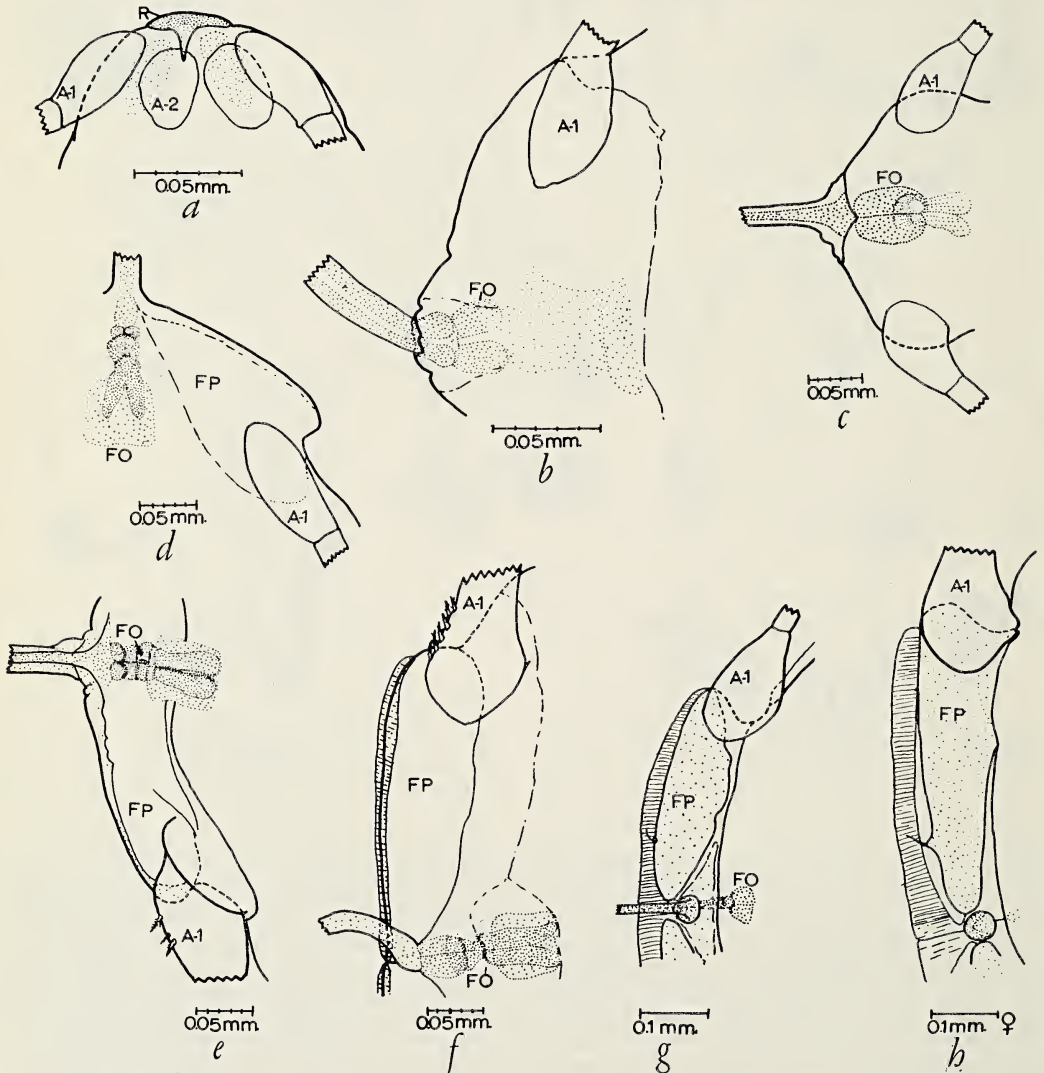


FIG. 13. Frontal region of developmental stages of *L. dissimulatus*. Ventral view of anterior surface: *a*, Copepodite; *b*, first chalimus; *c*, second chalimus; *d*, third chalimus; *e*, fourth chalimus; *f*, fifth chalimus; *g*, sixth chalimus; *h*, adult. A-1, Antennule; A-2, base of second antenna; FO, frontal organ; FP, frontal plate; R, Rostrum.

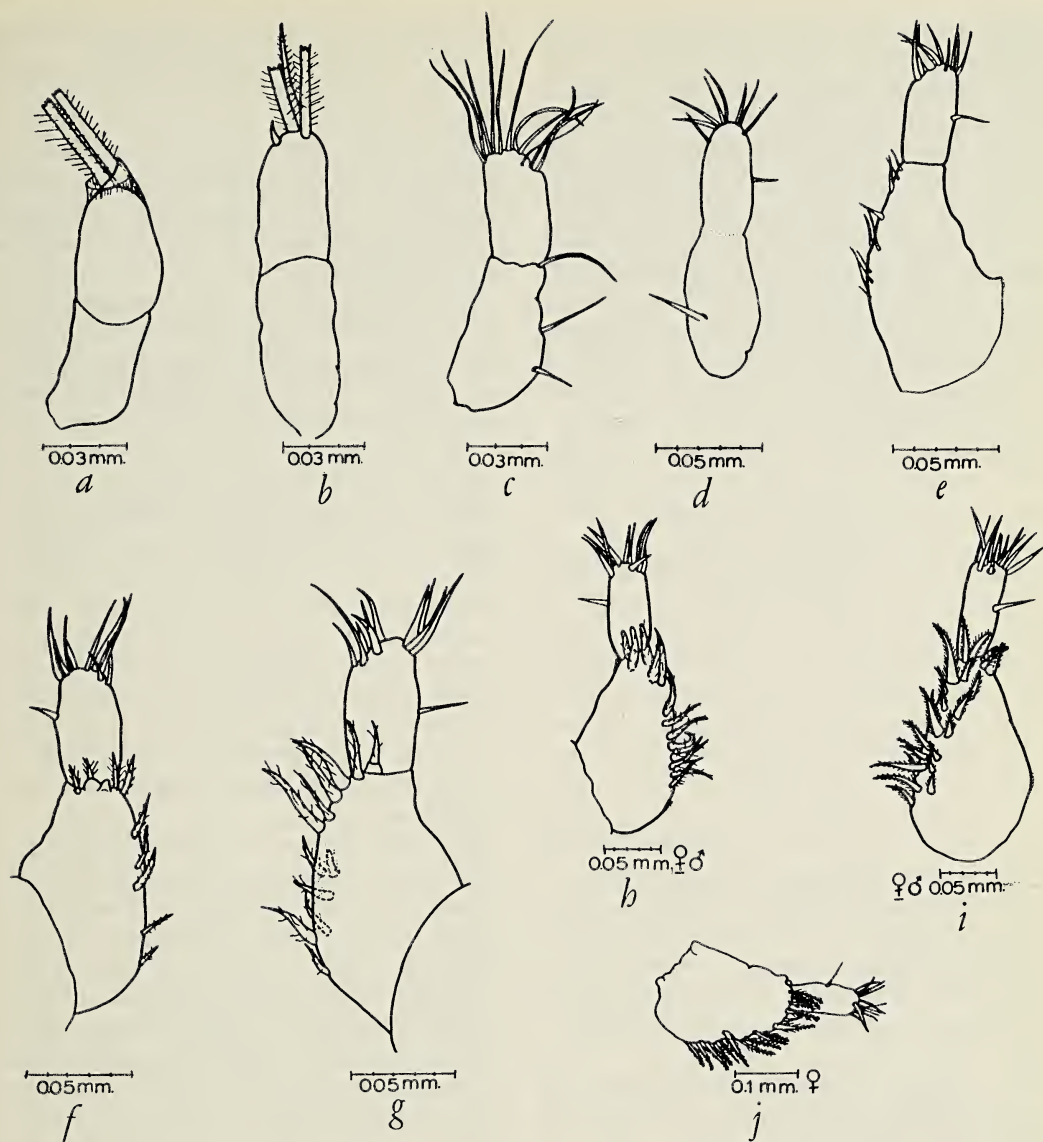


FIG. 14. Antennule of developmental stages of *L. dissimulatus* (ventral view). a, First nauplius; b, second nauplius; c, copepodite; d, first chalimus; e, second chalimus; f, third chalimus; g, fourth chalimus; h, fifth chalimus; i, sixth chalimus; j, adult.

margins of both segments are slightly irregular, more so in some specimens than in others. The first segment is slightly shorter than the second and is tapered rapidly in the proximal one-third to the narrow proximal end, the surface of attachment with the body. The second segment is tapered from the proximal to the slightly narrower, rounded distal end. The distal end of the second segment is encircled by a membrane pro-

jecting slightly past the segment. A broadly angled, heavily sclerotized process projects from the inner portion of the distal end of the second segment and two lightly plumose setae project from the inner portion of the distal end, adjacent to the process; these setae are slightly longer than the greatest length of the appendage.

The antennule of the second nauplius (Fig. 14b) is attached to the anterior ventral lateral

surface of the body. The first segment is now slightly longer than the second and its proximal end is almost pedunculate. The lateral margins of the segment are irregular although basically parallel; the distal end is slightly convex. The second segment possesses two long, lightly plumose setae, as in the first nauplius, but also a short, lightly plumose seta from the inner distal margin in addition to one short, spinelike process on the outer distal surface. The membrane present on the preceding stage is completely absent. The copepodite antennule is visible in late second naupliar specimens, incompletely filling the appendage; the character of the copepodite appendage is, however, not definable.

The antennule of the copepodite is attached to the ventral lateral surface just lateral to the rostrum. The first segment is almost $1\frac{1}{3}$ times the length of the second; its greatest width is approximately one-half the greatest length. The proximal anterior lateral margin (the margin that faces anteriorly in situ) of the first segment is strongly convex; the remaining lateral margin and the posterior lateral margin are somewhat irregular. The first segment possesses two naked setae from the middle of the anterior margin and one naked seta from the anterior distal margin. The division between the first and second segments is distinct although slightly irregular. The greatest length of the second segment is slightly less than the greatest width, the lateral margins are almost parallel, and the distal margin is irregular. The second segment gives rise to 11 naked setae from its distal surface.

The division between the two segments of the first chalimus antennule (Fig. 14d) is indistinct; the appendage is attached to the anterior ventral lateral surface just anterior to the indistinct, incomplete ventral groove dividing the frontal region from the cephalothorax. The first segment is slightly more than $1\frac{1}{2}$ times the length of the second, and the proximal region is broader than the distal; the rounded proximal end is almost included in the posterior margin, and the anterior and posterior margins are irregularly convex. A single naked seta is present on the proximal one-half of the anterior surface. The second segment is approximately twice as long as wide, the posterior and anterior margins are generally flatly convex, and

the distal end is rounded. A single naked seta is present on the middle of the posterior margin, as in the adult; eight naked setae are also present on the distal end.

The first chalimus antennule shows some degeneration from the copepodite appendage. This condition is evident in most of the appendages in the change that occurs from the copepodite to the first chalimus.

The division between the two segments of the second chalimus antennule (Fig. 14e) is distinct. The first segment is approximately twice the length of the second, comparatively longer than in the preceding stage. The proximal end of the first segment is broad; the segment is tapered irregularly to the narrower distal end. The anterior lateral margin is smoothly convex, longer than the irregularly concave posterior margin; the distal margin is flat. About 10 naked setules are present along the anterior lateral margin of the first segment. The second segment is twice as wide as long, the lateral margins are slightly irregular, and the distal margin irregularly rounded. A single naked seta is present on the middle of the posterior margin of the second segment in addition to nine naked setae on the distal surface.

The third chalimus antennule (Fig. 14f) is attached to a swelling on the posterior lateral portion of the tear-shaped frontal region. The greatest length of the first segment is about twice that of the second; its greatest width is two-thirds the length. The proximal end of the segment is angled; the anterior margin is thus more than twice the length of the posterior; the distal end is irregular and has two distinct swellings. Six lightly plumose setae arise from the anterior margin of the first segment and three from the distal margin. The second segment is slightly constricted at the junction of the first segment and curved convexly distally, causing the segment to appear club-shaped. The greatest width of the second segment is slightly more than one-half the length. As in the preceding two chalimus stages, a single naked seta is present on the middle of the posterior margin and nine naked setae arise from the distal surface.

The fourth chalimus antennule (Fig. 14g) is also attached to a swelling on the posterior lateral corner of the frontal plates which are now oriented more in a horizontal manner than

in the third chalimus. The general shape of the two antennular segments is similar to that of the preceding stage although the two distinct swellings present on the distal end of the first segment are now absent. The anterior surface of the first segment bears 10 setae that are distinctly plumose; the anterior distal surface bears two plumose setae. The second segment bears a single naked seta from the middle of the posterior margin, four from the posterior distal surface, and six from the anterior distal.

The antennule of the fifth chalimus (Fig. 14b) is attached in the same region as that of the fourth although the swelling at the junction of the appendage and the frontal region is not as distinct. The overlap of the antennule base onto the anterior ventral surface of the cephalothorax (see Fig. 13e-h) in the fifth and sixth chalimus and the adult may be due, at least in part, to the incorporation of the swollen portion of the frontal region into the frontal region of later stages and the resultant displacement of the posterior portion of the antennule base onto the cephalothorax. The attachment of the antennule thus appears to be basically on the frontal region and secondarily on the cephalothorax. The first segment of the fifth chalimus antennule is, with regard to the second segment, slightly longer than in the preceding stage, being more than twice the length of the second segment. The greatest width of the segment is slightly more than $1\frac{1}{2}$ times the length; the anterior margin is flatly convex medially and broadly rounded distally and proximally. The posterior margin is irregular, with a slight angular protrusion from the distal region. The anterior surface of the first segment bears 16 plumose setae, the distal surface three. The length of the second segment is approximately $2\frac{1}{2}$ times the width, the lateral margins are flatly convex, and the distal margin is rounded. The armature of this segment is the same as in the preceding stage.

The antennule of the sixth chalimus (Fig. 14i) is attached to the ventral lateral surface of the frontal region and is adjacent to or slightly overlaps the anterior ventral surface of the cephalothorax. The second segment is slightly longer than that of the preceding stage. The first segment is broad proximally, its greatest width being approximately five-eighths of the

greatest length, and tapers to the narrow distal end. The anterior margin is irregular except for the broadly convex proximal region, the posterior margin is shorter than the anterior, and the posterior surface bears a small distal protrusion. Nineteen plumose setae arise from the anterior surface of the first segment and the rounded distal surface bears five more. The second segment is club-shaped; the greatest width is slightly more than one-third the length. The lateral margins are generally flatly convex, the proximal end slightly narrower than the rounded distal end. The armature of the second segment consists of one naked seta from the middle of the posterior margin and 11 naked setae from the distal surface.

The antennule of the adult (Fig. 14j) is similar to that of the sixth chalimus except for the armature. The first segment has a small bifurcate protrusion on the posterior distal corner, the spines of which are crenate in the female and dentate in the male. The first segment bears 20 plumose setae on its anterior and distal surfaces; the second segment bears one naked seta on the middle of the posterior surface and 12 naked setae on the distal surface.

Second Antenna

In contrast to the antennule, the second antenna changes drastically during the life cycle of *L. dissimulatus*, from a biramous swimming appendage in the nauplius to a uniramous prehensile appendage in the adult.

The second antenna of the first nauplius (Fig. 15a) is biramous and attached to the ventral lateral surface just posterior to the base of the antennule. The protopodite is one-segmented, its greatest width approximately three-fourths of the greatest length. The lateral margins, except at the proximal end, are almost parallel; the distal margin is broadly curved. The five-segmented exopodite arises from the dorsal lateral surface of the protopodite, not from the distal end; the division between the exopodite and the protopodite is indistinct and incomplete. The first exopodite segment is slightly longer than the second, its proximal region tapered evenly to the narrow distal end. The second segment is tapered evenly from the proximal to the narrow distal end; a single lightly plumose seta is present on the inner distal lateral

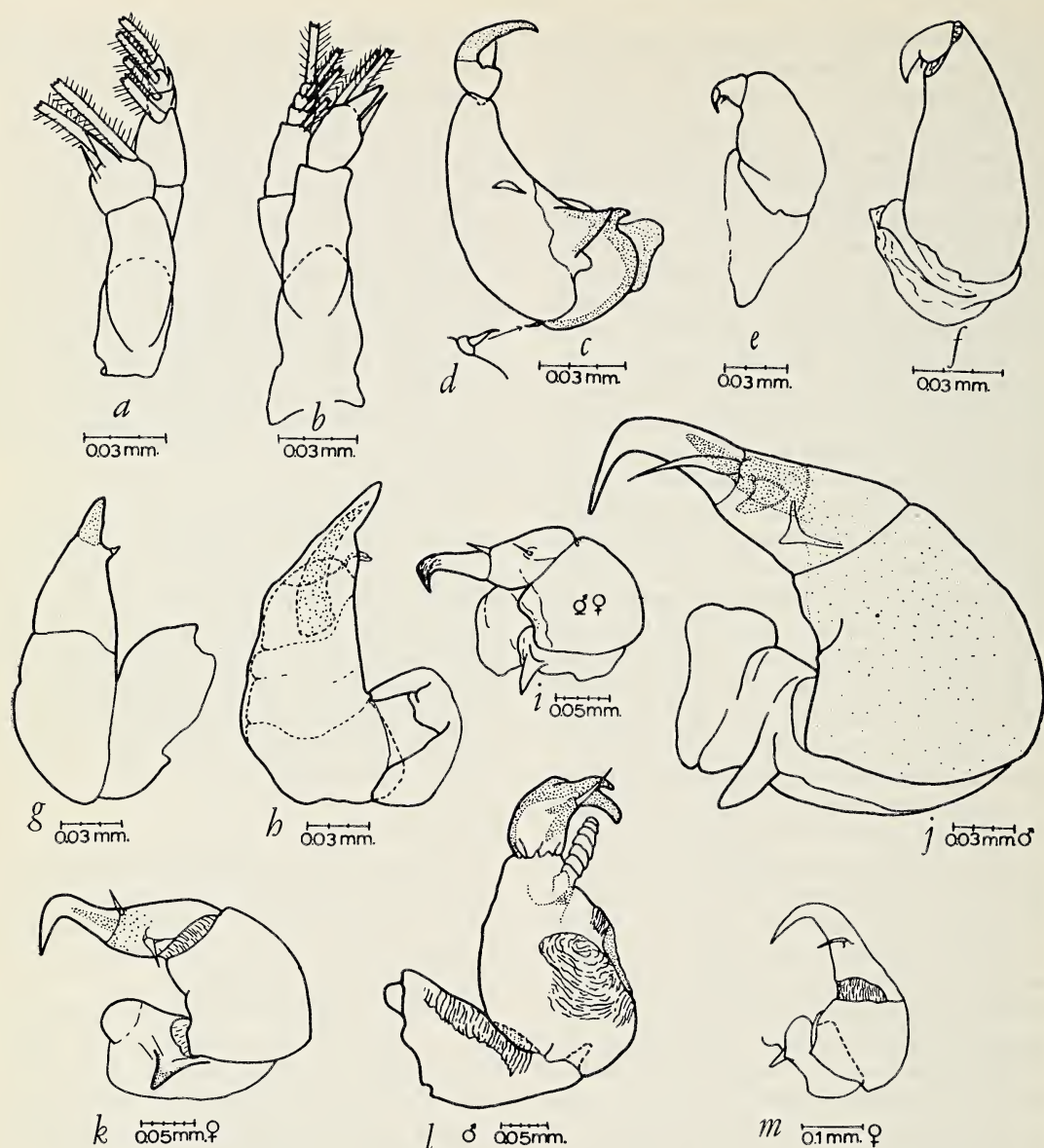


FIG. 15. Second antenna of developmental stages of *dissimulatus*. *a*, First nauplius, ventral view; *b*, second nauplius, ventral view; *c*, copepodite, posterior surface; *d*, setule of first segment of copepodite antenna (enlarged over original enlargement); *e*, first chalimus, posterior surface; *f*, second chalimus, posterior surface; *g*, third chalimus, posterior surface; *h*, fourth chalimus, posterior surface; *i*, fifth chalimus, posterior surface; *j*, male sixth chalimus, posterior surface; *k*, female sixth chalimus, posterior surface; *l*, male adult, posterior surface; *m*, female adult, posterior surface.

surface. The third segment is slightly more than one-third the length of the second; it is slightly wider distally than proximally and possesses a spinelike projection on the anterior proximal surface that extends distally slightly past the end of the segment. Further, the third segment

gives rise to a single lightly plumose seta from the inner lateral surface. The fourth segment is similar to the third although slightly smaller. The fifth segment is minute, its distal surface slightly irregular; the anterior lateral margin is longer than the posterior; a single lightly plu-

mose terminal seta is borne by this segment. The endopodite is two-segmented and attached to the ventral lateral surface of the protopodite. The division between the endopodite and protopodite is also indistinct and incomplete. The first segment is about 3 times the length of the second; its proximal end is narrow and the segment is curved slightly to the broader distal end. The lateral and distal margins of the second segment are continuous and form a broadly rounded margin. A strong spinelike projection is present on the middle of the distal end of the second segment and a slender spinelike projection is present on the posterior distal end. The second segment also bears two lightly plumose setae from its anterior distal surface.

The second antenna of the second nauplius (Fig. 15*b*) is similar to that of the first nauplius in general outline and make-up. The spinelike projections on the third and fourth segments of the first nauplius exopodite are absent in the second although the remaining armature is the same. The make-up and armature of the two endopodite segments is the same as that of the preceding stage with one exception: the two spinelike processes on the distal surface of the second segment appear to be more strongly developed.

The second antenna of the copepodite (Fig. 15*c, d*) is uniramous and three-segmented. The appendage is attached to the anterior ventral surface just medial to the posterior edge of the antennule base. Wilson (1905:542) indicates that the caligid second antenna is still biramous in the copepodite stage and Heegaard (1947: 56, fig. 14) describes and figures the reduced exopodite on the second antenna of *Caligus curtus*. Unless the small setule (Fig. 15*d*) or one of the projections on the proximal segment of the second antenna of *L. dissimulatus* is the remnant of the now absent ramus of the biramous second naupliar appendage, no evidence of a biramous condition is present. The first segment of the copepodite appendage is short and irregular, folded in several places, and possessing two backward-projecting, broadly-angled, spinelike processes, the proximal of which is poorly developed and the distal well developed. The division between the first and second segments is distinct although irregular. The second segment is broad proximally but tapered to a

narrow distal end; the lateral margins are regular, the distal surface concave. The second segment possesses a small lappet-like process projecting from the middle of the posterior medial surface. The third segment is short, less than one-eighth the length of the second; the proximal end is slender, the distal is broad, and both lateral margins are convex. The distal end of the third segment is flat except for a slight depression in the middle. A large spinelike terminal process curves anteriorly from the posterior one-half of the surface; a slender, seta-like accessory process projects from the anterior surface.

The first chalimus second antenna (Fig. 15*e*) appears to have degenerated somewhat; its shape is rather indistinct and the entire appendage appears flabby. The second antenna of this stage is attached just posterior and medial to the antennule base. The first segment is broad proximally, somewhat narrower distally, and the general outline is irregular. The distal end of the first segment forms an articulation surface for the second segment. The second segment is well developed; its greatest length is slightly more than the combined lengths of the first and third segments. This segment is broader proximally than distally, and the lateral margins are irregular, the outer longer than the inner; the distal surface faces inwards and its margin is generally flat. The third segment is short and truncate, tipped by a sharply curved, heavily sclerotized, spinelike process; the accessory process is present as a small seta-like structure on the distal one-half of the inner surface of the segment.

The second chalimus second antenna (Fig. 15*f*) is attached just posterior and medial to the base of the antennule. The first segment is broad and irregular in outline; its distal surface forms an articulation surface for the second segment. An indistinct, posteriorly directed, distally pointed process is present on the inner surface of the segment. The second segment is well developed, twice the length of the combined first and third segments. This segment is broad proximally and tapers to a narrow distal end. The outer lateral margins are smoothly convex, the inner irregularly concave; the distal surface is angled towards the inner proximal end, and the distal margin is slightly irregular. The outer margin of the third segment is convex and continuous with the outer margin of the short, in-

wardly curved terminal process. The inner margin of the third segment is broken by the lobe-shaped proximal region. The division between the terminal process and the segment is indistinct. In addition to the terminal process, a small seta-like accessory process is present on the lobate inner proximal region.

The second antenna of the third chalimus (Fig. 15g) appears to have degenerated even more when compared with the same appendage on the copepodite and the previous two chalimus stages. This condition is a continuation of the trend initiated in the first chalimus, a gradual loss of rigidity and distinct form before the development of the adult appendage. To exemplify this loss of form, the segments of the third chalimus appendage are distinct but plastic in nature, the integument is flabby, and the ridges and grooves present on the second antenna of one side of a specimen are often absent on the other; further, the sclerotization of the terminal process appears reduced. The greatest length and width of the first and second segments of the second antenna of the third chalimus are approximately equal although the shape is different. The distal end of the first segment is generally concave, of the second segment almost flat. The third segment is slightly shorter than either of the preceding two and is tapered from the broad proximal to pointed distal end. The inner margin of the segment possesses a distinct protrusion on the distal one-half that is tipped by a short, pointed process. The more heavily sclerotized terminal process of the succeeding stage is visible inside the distal portion of the third segment.

The second antenna of the fourth chalimus (Fig. 15b) is similar in general make-up to that of the preceding stage except that the first segment is not as long. Further, it has a flaplike structure projecting distally from the proximal end; one specimen also possessed a triangular, distally directed flap that appeared to correspond to the posteriorly directed, pointed process on the first segment of the adult female. The length of the second segment is greater than that of the first, the division between the second and third segments is indistinct, and the lateral margins of both segments are irregular. The distal inner margin of the third segment bears a small, lobate process that will become the accessory

process of the adult and is the protrusion that was present on the same region of the previous stage. The distal end is bluntly pointed, more heavily sclerotized than the preceding stage but not as heavily as the terminal process of the fifth chalimus, visible inside the fourth.

The second antenna of the female and male fifth chalimus (Fig. 15i) are similar. The general appearance of the adult female appendage is now beginning to manifest itself in the females of this stage. The first segment is irregular, the distal surface concave and forming the articulation surface for the second segment. A spinelike, posteriorly directed process is present on the posterior surface of the segment. The second segment is short and strongly developed; the inner margin is convex, approximately 3 times the length of the concave outer margin due to the angled distal and proximal surfaces. The distal surface of the second segment is irregular; the inner portion is concave, the outer convex although both portions are heavily sclerotized and form the articulation surface for the third segment. The third segment and terminal process in both sexes is approximately $1\frac{1}{2}$ times the length of the second segment; the proximal surface is lobate and articulates in the concavity of the distal end of the second segment. The terminal process of the third segment is curved inwards strongly at the distal end; the division between the process and the segment is indistinct. Further, two seta-like accessory processes are now present, one on the posterior proximal region, the second on the inner distal region.

The second antenna of the sixth chalimus (Fig. 15j, k) is similar in both sexes. The first segment is slightly longer in the male but, for both male and female, is short and the entire distal surface is concave, forming an articulation surface for the second segment. The first segment is irregular in outline, the outer surface appearing platelike and tapered gradually to the distal surface, the inner surface somewhat irregular, with a posteriorly directed, spinelike projection that is more distinct than in the previous stage. The second segment is strongly developed, its greatest width slightly more than four-fifths of the greatest length; the outer margin is flatly convex, longer than the irregularly concave inner margin. The width of the distal

end of the second segment is slightly less than three-fourths of the width of the proximal end; the distal surface is concave with its outer portion heavily sclerotized and serving as the articulation surface for the outer proximal end of the third segment. The third segment and terminal process are similar to those of the preceding stage although the process is slightly longer and the distal portion more sharply curved. The adult female and male appendage is visible within the second antenna of late sixth chalimus specimens. Both parts of the bifurcate terminal process of the adult male can be seen (Fig. 15j) as well as the single female terminal process (Fig. 15k).

It was earlier stated that the second antennae can not be used to differentiate the two sexes in the late chalimus of *L. dissimulatus*. As was just described, the female and the male second antenna are similar in the sixth chalimus, the last larval stage. Not until the moult from the sixth chalimus to the adult is there any significant difference between the appendages of the two sexes in *L. dissimulatus*. For this reason, the presence or absence of the sixth legs, found only in the male, was used as the major differentiating characteristic. Additionally, in the sixth chalimus, the presence of internal spermatophores in the male was used to verify the differentiation of the two sexes.

The second antenna of the adult (Fig. 15l, m) is attached to the ventral surface of the cephalothorax just anterior and medial to the postantennal process and posterior and lateral to the base of the antennule. The first segment of the female is short and forms a broad articulation surface for the second segment. The segment possesses a posteriorly directed, spinelike projection from the posterior proximal surface. The second segment is strongly developed, its greatest width being equal to its greatest length. The third segment is slender and heavily sclerotized, bearing a sharply curved, spinelike terminal process and two naked, seta-like accessory processes, one from the inner surface of the proximal region and the second from the distal lateral surface. The division between the third segment and terminal process is indistinct and incomplete.

The first segment of the adult male second antenna (Fig. 15l) is longer than that of the

female; the segment is broader proximally than distally and is attached to the cephalothorax along the entire length of the proximal surface. The distal end of the first segment is small and two-pronged, forming an articulation surface for the second segment. Additionally, the major portion of the outer lateral surface forms an adhesion surface of heavily sclerotized, overlapping, platelike structures. The second segment is strongly developed, its greatest width slightly more than one-half of the greatest length. The outer margin of the segment is strongly convex proximally; the inner margin is irregular due to the presence of two sets of adhesion surfaces similar to those of the first segment. The inner distal margin of the second segment also possesses a finger-like protrusion that appears to be segmented but presumably forms an adhesion surface, and the segmented appearance is due to the overlapping plates. The protrusion is, in most specimens, curved around the second segment and appears as a regular adhesion surface but it is not attached to the segment except at its proximal end. The third segment is short and bears a bifurcate terminal process in addition to a single, naked, seta-like accessory process from the inner distal end.

Mandible

Comparing the over-all development of the three naupliar appendages, it is evident that the mandible has the most drastic change. Almost all of the change occurs in the moult from the second nauplius to the copepodite when the appendage changes from a biramous appendage to a uniramous, four-parted, rodlike process. The four-parted condition could not be traced to either the exopodite or the endopodite of the naupliar appendage. All four parts appear to be almost completely fused; there are no muscles penetrating the appendage and there is no trace of the second ramus of the biramous naupliar appendage. These three conditions make the analysis of the derivation of the mandible of the copepodite of *L. dissimulatus* extremely difficult, and even with the analysis made by Heegaard (1947:59, 196–202), no hypothesis can be offered until further work has been done.

The mandible of the first nauplius (Fig. 16a) is biramous and attached to the ventral lateral surface just posterior to the second antenna.

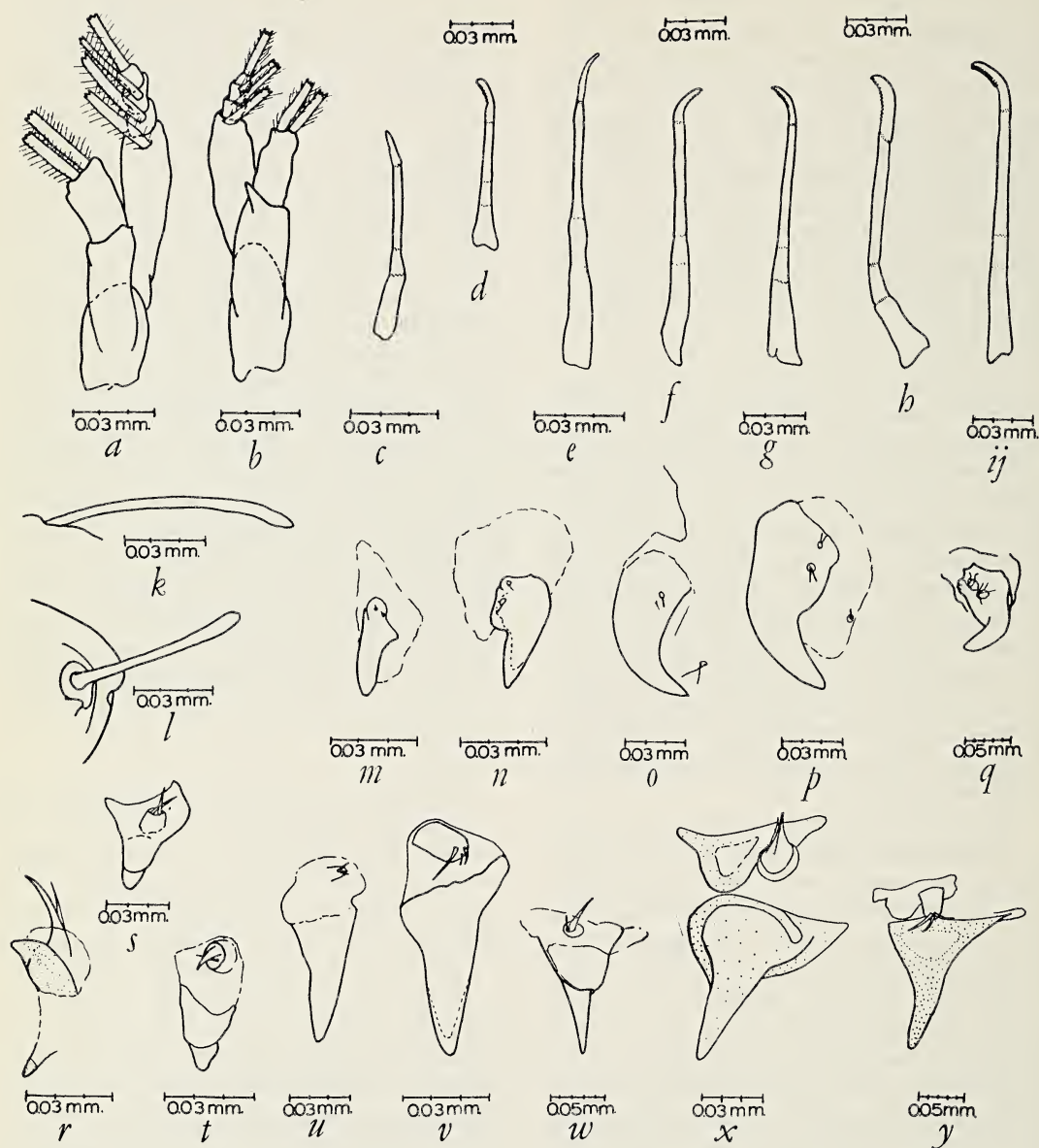


FIG. 16. Mandible, postantennal and postoral processes of developmental stages, in addition to balancers of naupliar stages of *L. dissimulatus*. *a-j*, Mandible: *a*, First nauplius, ventral view; *b*, second nauplius, ventral view; *c*, copepodite; *d*, first chalimus; *e*, second chalimus; *f*, third chalimus; *g*, fourth chalimus; *h*, fifth chalimus; *i, j*, sixth chalimus and adult. *k, l*, Nauplius balancers: *k*, First nauplius, dorsal view; *l*, second nauplius, lateral view (also posterior end of body of nauplius). *m-q*, Postantennal process: *m*, Third chalimus; *n*, fourth chalimus; *o*, fifth chalimus; *p*, sixth chalimus; *q*, adult. *r-y*, Postoral process: *r*, Copepodite; *s*, first chalimus; *t*, second chalimus; *u*, third chalimus; *v*, fourth chalimus; *w*, fifth chalimus; *x*, sixth chalimus; *y*, adult.

The protopodite is one-segmented, its greatest width about three-fourths of the greatest length; the lateral margins are slightly irregular although generally convex, and the distal margin is broadly curved. The exopodite is four-segmented and attached to the dorsal lateral surface of the protopodite although the division between the first segment and the protopodite is incomplete. The first segment of the exopodite is more than $2\frac{1}{2}$ times the combined lengths of the remaining three segments, its lateral margins are broadly convex, and the distal surface has a concavity in which the proximal end of the second segment is attached. A single lightly plumose seta is present on the distal portion of the inner lateral surface of the first segment. The second segment is short, its greatest width about equal to the greatest length; the distal surface is slightly concave and receives the proximal end of the third segment. A single seta is present on the distal portion of the inner lateral surface of the second segment. The third segment is slightly longer than the second and flared from the narrow proximal to broader distal end; the distal surface also has an irregular concavity for the proximal end of the fourth segment. A single seta is present on the distal portion of the inner lateral surface of the third segment. The fourth or terminal segment is minute and rodlike, with a concave distal surface that receives the base of the slightly plumose terminal seta. The endopodite is two-segmented and attached to the ventral lateral surface of the protopodite although the division between the first segment and the protopodite is incomplete. The first segment is approximately $1\frac{1}{3}$ times the length of the second, the lateral margins are slightly irregular, and the distal end is flared slightly and bearing a small, pointed protrusion on the anterior distal corner. The second segment has slightly irregular lateral margins, the distal end is slightly broader than the proximal, and the distal surface is flat and bears two lightly plumose setae.

The mandible of the second nauplius (Fig. 16*b*) is similar to that of the first nauplius. The first segment of the exopodite is, however, longer than that of the preceding stage, being more than $3\frac{1}{2}$ times the combined lengths of the remaining three segments. The small pointed protrusion on the anterior distal corner of the

first endopodite segment of the first nauplius is larger in the second nauplius and projects anteriorly although there is some variation in size in different specimens.

The copepodite mandible (Fig. 16*c*) is uniramous and four-parted as in the adult. The appendage is attached to the ventral surface of the cephalothorax just lateral to the division between the well-developed membranous hyperstome and hypostome and projects through the division into the mouth cone. All four parts are heavily sclerotized and indistinctly divided, the division often appearing only as a light area. The first part is approximately twice the length of the second, tapered slightly from the proximal to the narrower distal end. The second part is strongly tapered from the first to slender third part. The third part is elongate, the length slightly less than the combined lengths of the first two parts; the lateral margins are almost parallel. The fourth part is short, the length less than one-half that of the third part. The fourth part is also angled medially; there is no curvature as the fourth part of later stages has. The fourth part is tapered to a sharp point distally; the inner margin is lightly serrated but does not have the denticulations visible in the adult.

The condition exhibited by the copepodite mandible is changed but little in the chalimus stages. The only part that changes to any extent is the fourth part, the other three changing only slightly in their relative lengths. A slight curvature of the fourth part is visible in the first chalimus (Fig. 16*d*), this curvature becoming greater throughout the remaining chalimus stages (Fig. 16*e-i*) so that the fourth part is evenly curved in the sixth chalimus and adult (Fig. 16*i, j*). Further modification of the fourth part is from the sharply pointed condition of the copepodite to the bluntly rounded tip of the adult and the gradual appearance of the denticulations present on the inner surface of the adult.

Mouth Cone

The mouth cone is first exhibited by the copepodite, although a slight swelling is visible on the second nauplius that may be the beginning of this structure. The cone itself is formed of two membranous structures, a hyperstome and hypostome, that are usually closely applied

to each other or overlap slightly. A slight opening is visible in the proximal portion through which the mandibles project into the cone. Relatively little change occurs in the mouth cone from the copepodite to the adult although because of the size and nature of the cone, a complete analysis was not made. In the adult, however, both the hyperstome and hypostome possess several heavily sclerotized strengthening regions on their lateral surfaces. The distal end of the cone is membranous, very flexible, and finely setuliferous.

Postantennal Process

The postantennal process is discussed after the mandible because of the possibility that it is a true appendage (Heegaard, 1947:59, 203-206). The terminology used, with regard to the author's present beliefs, is the same as that used in Lewis (in press). The fact that, in *L. dissimulatus*, this process does not appear until the third chalimus, long after all of the other oral appendages are present, is an indication that it is not a true appendage, although Heegaard (1947:205) presents a hypothesis for its late appearance. The arguments both for and against the term "appendage" being applied are, however, strong enough so that this author prefers not to commit himself until further studies can be made.

The postantennal process of the third chalimus (Fig. 16*m*) is a blunt-tipped, spinelike process projecting posteriorly from an indistinct plate on the ventral surface of the cephalothorax posterior and lateral to the base of the second antenna. The proximal end of the process bears two minute nodules, each with one setule.

The postantennal process of the fourth chalimus (Fig. 16*n*) is more strongly developed and sharply pointed than that of the preceding stage. The indistinct plate still bears the process, from the base of which arise two minute nodules as in the preceding stage, each with a single setule.

The postantennal process of the female and male fifth chalimus (Fig. 16*o*) is more strongly developed than in the preceding stage; the process has become distinctly curved medially and, in addition to the two single setule-bearing nodules on the proximal end, now has a third nodule just medial to the distal region of the proc-

ess. The plate from which the process of the preceding two stages arose is now almost completely invisible.

The postantennal process of the female and male sixth chalimus (Fig. 16*p*) is curved medially as in the preceding stage. The proximal region is, however, more developed, the inner margin irregular, not evenly curved as in previous stages. Two nodules are present on the proximal end but, in contrast to the last three stages, each now bears two fine setules. Only one setule was visible on the third nodule, although the extremely small diameter and short length of the setules made observation difficult and the number may be incorrect. The plate from which the process arises is more distinct than in the preceding stage.

The adult female and male postantennal process (Fig. 16*q*) is similar to that of the sixth chalimus, although the distal end is more sharply curved. The proximal nodule of the two nodules on the base of the process now gives rise to three setules, the distal nodule to four. The third nodule of the chalimus stages did not appear to be present.

Postoral Process

The postoral process is of the same general make-up as the postantennal process, although it is first present on the copepodite instead of the third chalimus. The process has been called the first maxilla and the second maxilla. Its structure, in addition to the location of the origin of the subesophageal ganglionic nerve that innervates it (adjacent to nerves that go to the lateral musculature and the postantennal process) and the inability to determine its anlage, has caused the author to use the term "postoral process."

The postoral process of the copepodite (Fig. 16*r*) consists of a posteriorly projecting, well-developed, distally pointed process and two setule-like projections just medial to the proximal end of the process. Both the process and the projections arise just lateral and slightly posterior to the base of the mouth cone. The inner margin of the process is convex, the outer concave with a slight proximal swelling. A minute, heavily sclerotized, lobelike structure is present just lateral to the process and appears to be con-

nected to the same poorly defined plate from which it arises.

The postoral process of the first chalimus (Fig. 16*g*) is distinctly different from that of the copepodite. The process consists of a two-parted, spinelike process and a setule-bearing nodule, both attached to a well-defined plate just lateral and posterior to the base of the mouth cone and contiguous with the plate present at the base of the cone. The two-parted, spinelike process projects posteriorly; both parts are rounded distally, the second part being attached to the distal end of the first. The greatest length of the second part is approximately two-thirds that of the first. The setule-bearing nodule is just anterior to the base of the spinelike process, at the anterior end of the plate. The nodule is small and gives rise to two slender setules from its distal surface.

A general transition is apparent from the first chalimus to the adult. The two-parted condition of the postoral process is still evident in the second chalimus (Fig. 16*h*), but in the third (Fig. 16*i*) the two parts become fused, the distal portion becomes more sharply pointed, and the base spreads out to its greatest width, in the adult (Fig. 16*j*), the width in the adult being just slightly less than the length. The plate from which the process and the setule-bearing nodule arise becomes indistinct in the second chalimus, third chalimus, and fourth chalimus, then becomes more distinct in the fifth chalimus but appears as two parts. These two parts of the plate are evident in the sixth chalimus and in the adult. The anterior plate has a posteriorly directed lobe (within, not projecting from, the cephalothorax) just medial to which the setule-bearing node projects. The posterior plate forms the base of the spinelike process and is continuous with it. The setule-bearing node enlarges somewhat throughout development and adds another setule to its armature, having two slender setules in the second chalimus, three in the third and fourth chalimus, two (?) in the fifth, and three in the sixth chalimus and in the adult. All the setules are borne on the distal surface of the nodule.

Maxilla

The term "maxilla" is applied to the pair of oral appendages immediately behind the mouth

cone and postoral processes. This appendage pair has gone under a variety of names because of the terminology applied to the postantennal and postoral processes. Inasmuch as the term "process" is here applied to the postantennal and postoral structures, the first pair of recognizable appendages behind the mouth are designated as the maxillae.

The maxilla is first present in the copepodite (Fig. 17*a*) and is found attached to the ventral surface of the cephalothorax just posterior and lateral to the postoral process. The first segment of the two-segmented structure is strongly developed; the proximal surface possesses a medial projection that articulates with the cuticle of the body at the point of attachment of the appendage. The distal margin of the first segment is flat; the surface is depressed and receives the proximal surface of the second segment. The second segment is elongate, being slightly longer than the first segment and much thinner. The lateral margins of the second segment are irregular, the outer proximal margin curving inward to the irregular proximal surface, the inner margin with several flatly convex swellings. The distal region of the second segment is slightly swollen, the distal margin broadly rounded. Two processes are present on the distal region and extend out from the segment. The outer process is spinelike and is less than one-fourth the length of the segment; this process possesses a series of minute, tine-like projections along the inner margin giving it a brushlike appearance. The inner process arises from the posterior lateral surface of the distal region, not the distal surface as does the outer process; it is lobate and flimsy in nature, its length approximately equal to that of the outer process.

The segments of the maxilla of the first chalimus (Fig. 17*b*) are similar in general make-up to those of the copepodite. The proximal articulation surface of the copepodite appendage is, however, absent in the first chalimus and, further, the first segment is somewhat thicker. The distal surface of the first segment is concave and forms the articulation surface for the ball-shaped proximal end of the second segment. The inner of the two terminal processes on the second segment is slightly longer than the outer and is tapered to a sharp point. The outer of the two processes is simple and lobate, lacking

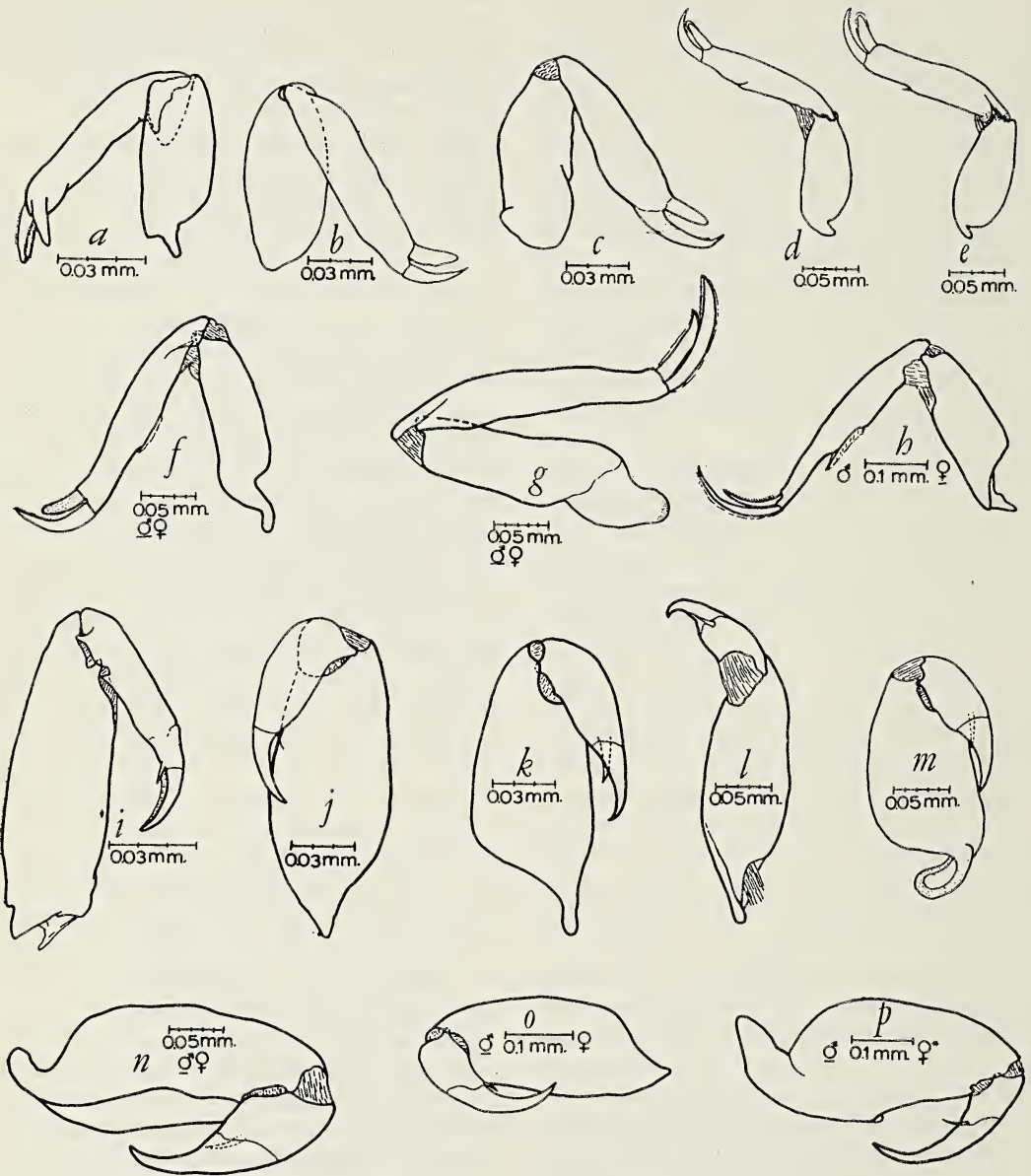


FIG. 17. Maxillae and maxillipeds of developmental stages of *L. dissimulatus*. *a-b*, Maxillae: *a*, Copepodite; *b*, first chalimus; *c*, second chalimus; *d*, third chalimus; *e*, fourth chalimus; *f*, fifth chalimus; *g*, sixth chalimus; *h*, adult. *i-p*, Maxillipeds: *i*, Copepodite; *j*, first chalimus; *k*, second chalimus; *l*, third chalimus; *m*, fourth chalimus; *n*, fifth chalimus; *o*, sixth chalimus; *p*, adult. For minor differences between male and female adult maxilliped, see description of appendage.

the series of tine-like projections of the copepodite process. The arrangement of the terminal processes thus appears to be reversing itself and, as will be described for later stages, does reverse so that the inner process is complex and the outer simple.

The second chalimus maxilla (Fig. 17c) appears to have degenerated slightly from that of the preceding stage. The shape varies somewhat in different specimens and, in general, appears to be of a rather plastic nature. The first and second segments are of approximately equal length, the first appearing more strongly developed than the second. The outer proximal corner of the first segment is heavily sclerotized and appears to function as an articulation surface. The distal end of the first segment is slightly narrower than the proximal, and the lateral margins are somewhat irregular; the distal region is heavily sclerotized on the inner portion although no distinct articulation surfaces are visible. The second segment is narrower proximally than distally, the segment appearing almost club-shaped. The proximal margin of the segment is almost included in the inner lateral margin, both lateral margins are somewhat wavy, and the distal margin is rounded. The inner terminal process is relatively longer than in the preceding stage, now being approximately twice the length of the outer process; further, the process is tapered to a sharp point and possesses several minute setules on the distal end of the outer margin. The inner terminal process is simple and lobate, almost identical to that of the first chalimus.

The maxilla of the third chalimus (Fig. 17d) differs somewhat from that of the second chalimus. The first segment is approximately two-thirds the length of the second, its proximal end projecting as a curved, lobate process that serves as an articulation surface. The outer lateral margin is broadly convex, the inner flatly convex; the greatest width is slightly less than one-half of the greatest length and the general shape of both of the segments appears to be more distinct than in the preceding stage. The distal margin of the first segment is irregular and heavily sclerotized, the irregularities serving as articulation surfaces for the proximal end of the second segment. The second segment is slender, and the inner and outer margins are generally

flatly convex. The proximal margin of the second segment is now completely included in the inner margin. The proximal surface possesses two small knoblike projections with a concave surface between them; both of the projections and the concave surface articulate with reciprocal processes on the irregular distal end of the first segment. The middle of the inner margin of the second segment now has a short groove extending from the surface inward and proximally; this groove corresponds to the position of one of the spines present on the adult appendage. The distal end of the segment is tapered to a medial point and possesses the two terminal processes present on preceding maxilla-bearing stages. The inner of the two processes now curves sharply outward, over the distal end of the outer process, and is minutely frilled along its outer distal margin. The outer process is lobate, approximately two-thirds the length of the inner process; the distal margin bears a fine membrane.

The maxilla of the fourth chalimus (Fig. 17e) still bears the somewhat degenerate appearance of the third chalimus appendage. Except for the distal end, the first segment is similar to that of the preceding stage. The outer distal margin of the segment is concave; the distal end of the inner lateral margin is also concave, forming a knoblike projection at the junction of the two which is heavily sclerotized. The proximal surface of the second segment, included in the inner lateral surface, is bilobed. The bilobed condition of the surface appears to be due to a split or division occurring in the small concavity separating the two heavily sclerotized knobs of the previous stage. The separation between the two lobes forms an articulation surface for the knoblike projection of the inner distal surface of the first segment and the lobes themselves articulate in the concavities on the distal and inner distal lateral surfaces of the first segment. The middle of the inner lateral margin of the segment is indented in the region of the groove of the preceding stage and bears a single spinule. The second segment is tapered slightly from the indentation to the distal end, which is tipped by the two terminal processes. The inner terminal process is similar to that of the preceding stage, the outer process is slightly longer, and the fine membrane now extends

around the distal end and distal lateral margins.

Both segments of the maxilla of the fifth chalimus female and male (Fig. 17f) are more slender and appear more elongate than those of the preceding stage. The first segment is slightly shorter than the second and its proximal end projects as an irregular, lobate articulation process. The outer margin of the segment is flatly convex; the inner is slightly convex proximally, flat medially and concave distally. The outer distal margin is tapered abruptly to a knoblike projection of the inner distal surface that appears to be the enlarged projection of the distal end of the first segment of the fourth chalimus. The second segment is slender, the proximal end two-parted and included in the inner lateral margin. The junction of the two parts of the proximal end forms a concave surface that articulates on the knoblike process on the distal end of the first segment. The outer lateral margin of the second segment is generally flatly convex; the inner lateral margin is slightly irregular, with a slight indentation in the middle that bears a single spinule and a fine membrane connected to the spinule and extending proximally for a short distance. The distal end of the second segment is almost flat and bears two terminal processes. The inner terminal process is relatively longer than in the preceding stage, being $1\frac{1}{2}$ times the length of the outer process; the outer margin is fringed with a fine, lightly frilled membrane. The outer process is lobate and covered with minute, hairlike projections.

The maxilla of the female and male sixth chalimus (Fig. 17g) is similar to that of the fifth chalimus in general shape. The segments, and especially the proximal projection of the first segment, are heavier; the knoblike projection of the inner distal surface is on the inner corner so that it forms the junction of the inner lateral and inner distal surfaces. The proximal end of the second segment, included in the inner lateral surface, again appears two-lobed, the proximal lobe extending proximally and forming the point of attachment for the muscle that abducts the second segment. The distalmost of the two lobes forms an indentation in the margin that extends for a short distance although there is a continuation, as a distinct line of division between the two lobes, running almost parallel to the lateral margins of the segment.

The middle of the lateral surface of the second segment is tapered slightly but abruptly; the spinules and membrane present in this region in the adult and in the preceding stage were not present on any of the specimens examined. The two terminal processes on the flat distal end of the second segment are both slightly larger than in the preceding stage; the outer is now pointed distally and both have a fine, membranous margin along their inner and outer surfaces.

The maxilla of the adult female and male (Fig. 17h) is more definitely shaped than any of the preceding stages and the first segment more strongly developed than in the preceding two chalimus stages. The first segment is short and stocky, the inner proximal end protruding as an irregular articulation surface. The distal lateral margins of the first segment are tapered irregularly to the somewhat narrow distal surface, the median portion of which projects as a narrow, lobate articulation surface that is heavily sclerotized. The second segment is elongate, the lateral margins irregularly convex. The proximal surface, included in the inner lateral surface, is irregular, with a slight concavity that forms the place of articulation for the medial projection of the distal surface of the first segment. The middle of the inner margin is notched in two places, the proximal notch bears a minute spine not present in any preceding stage, and the distal notch bears a larger spine, about twice the length of the proximal spine. A fine membrane is also present and connects the two spines. The two terminal processes arising from the step-shaped distal end of the second segment are more elongate than those of the preceding stage. The innermost of the two processes is about $1\frac{1}{2}$ times the length of the outer and possesses a membrane along the outer margin. The outer process is fringed by a frilled membrane along the outer margin.

Maxilliped

The maxillipeds have been termed the first thoracic appendages in copepods as well as in other crustaceans and the maxillae as the last cephalic appendages (Borradaile et al., 1958: 347-348). This terminology is accepted by most authors, including those who apply the term "first maxilla" to the postoral process, but is not accepted by those workers who call the post-

antennal process the first maxilla and the postoral process the second maxilla. In this latter case the first pair of identifiable appendages behind the mouth thus become the first maxillipeds and the last pair of appendages before the thoracic legs become the second maxillipeds. With the use of the term "maxilla" for the first pair of identifiable appendages behind the mouth, the term "maxilliped" is here applied to the pair of appendages anterior to the first thoracic legs.

The maxillipeds are first present in the copepodite (Fig. 17*i*) as uniramous, two-segmented appendages attached to the ventral surface of the cephalothorax posterior and slightly medial to the base of the maxillae. The first segment is slightly less than twice the length of the second; its proximal end is broad and has a poorly developed articulation surface that projects from the middle of the surface. The lateral margins of the first segment are slightly curved, the anterior margin flatly concave, the posterior flatly convex; the distal anterior margin is tapered sharply inward to the narrow distal end. Both the distal and inner distal lateral surfaces have several rather heavily sclerotized projections and depressions, each fitting depressions or receiving projections from the proximal surface of the second segment. The second segment is slender, the inner margin shorter than the outer although both are slightly irregular. The distal region of the second segment is tapered to the short distal surface which bears a strongly developed, spinelike terminal process that curves medially evenly. A slender, short, spinelike structure is present as an accessory process and arises from the inner distal surface of the segment. The division between the segment and the terminal process is distinct and complete, that between the segment and accessory process indistinct and incomplete; the terminal process bears a membranous fringe along the inner margin.

The first chalimus maxilliped (Fig. 17*j*) is more strongly developed than in the copepodite. The first segment is approximately the same length, with regard to the second segment, although appearing heavier, its width being slightly greater than one-third of its length. The inner proximal surface of the first segment projects as a tapered articulation process, and the lateral margins of the segment are flatly convex,

the outer margin longer than the inner; the distal surface is angled inward and downward and possesses two distinct, heavily sclerotized articulation surfaces for the second segment. The second segment, including the terminal process, is tapered from the broad proximal to pointed distal end. The proximal region of the segment has two lobate projections, one from the anterior surface and the second from the posterior, which articulate with the indentations of the distal surface of the first segment. A small seta-like accessory process arises from the inner surface of the segment, at the distinct junction of the segment and the terminal process. The terminal process is heavily sclerotized, curves inward, and lacks the marginal membrane of the previous stage.

The changes that occur in the maxilliped from the first chalimus to the adult (Fig. 17*k-p*) are relatively minor. The general shape remains the same and the armature of the second segment does not change. The articulation surface that projects from the proximal region changes slightly, becoming somewhat longer in the second chalimus (Fig. 17*k*) and then gradually curving in the third chalimus (Fig. 17*l*) and fourth chalimus (Fig. 17*m*) until it becomes almost recurved in this and the fifth chalimus stages. The articulation projection then becomes lobate in the sixth chalimus (not visible in Fig. 17*o*) and the adult (Fig. 17*p*). The inner surface becomes grooved in the fifth chalimus and remains that way up to and including the adult. The division between the second segment and terminal process becomes rather indistinct in later stages of development. The adult male maxilliped has a small shelflike structure that is present on the middle of the inner margin of the first segment. This structure appears in the last moult, from the sixth chalimus to the adult, and is the only apparent difference between the maxilliped of the female and the male.

Sternal Furca

The sternal furca is a single process between and slightly posterior to the maxilliped bases and is another structure about which little is known. Most authors have simply reported its presence or absence and utilized this as a taxonomic characteristic. The position of the structure, posterior to the maxilliped bases, does not

allow any specific interpretation as to its origin. If the maxillipeds are the first pair of thoracic appendages, the sternal furca may be the remnant of the sternal plate which exists between the first three pairs of thoracic legs of *L. dissimulatus* and many other caligoids. No definitive evidence for this idea can be offered, however, other than the relative position to the

maxillipeds and the presence of sternal plates on some of the thoracic legs. Furthermore, the sternal furca in *L. dissimulatus* does not appear until the fourth chalimus, long after the maxillipeds, the thoracic legs, and the sternal plates of the first two thoracic legs. The hypothesis has, therefore, at least one pitfall unless, and no information is given to support this, a shift can

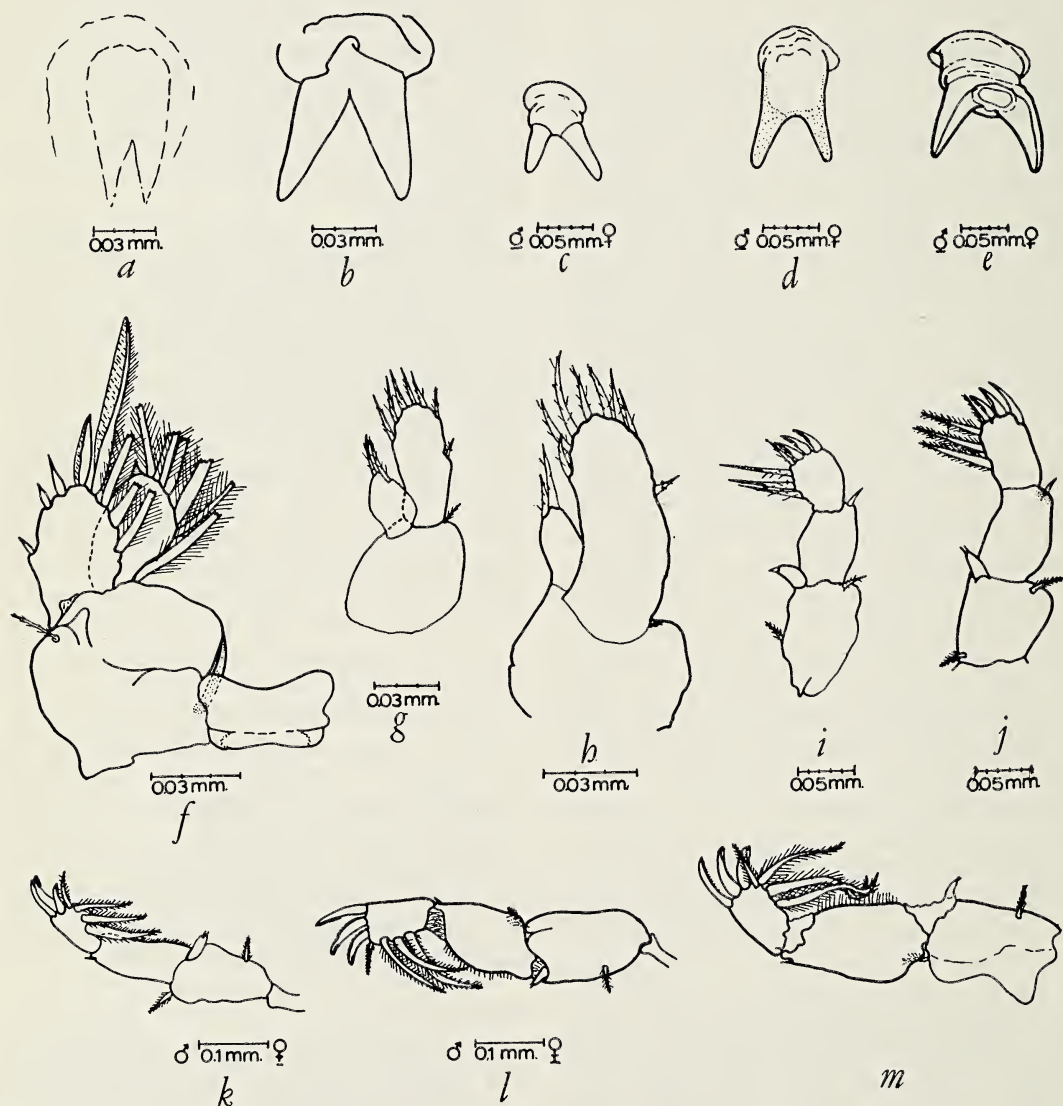


FIG. 18. Sternal furcae and first thoracic legs of developmental stages of *L. dissimulatus*. *a-e*, Sternal furcae: *a*, Third chalimus; *b*, fourth chalimus; *c*, fifth chalimus; *d*, sixth chalimus; *e*, adult. *f-m*, First thoracic legs: *f*, Copepodite; *g*, first chalimus; *h*, second chalimus; *i*, third chalimus; *j*, fourth chalimus; *k*, fifth chalimus; *l*, sixth chalimus; *m*, adult.

occur in the time that a structure appears in development. If this were possible, then the status of the postantennal process must also be reviewed. The presence of a short but distinct muscle that is attached to the sternal furca and the mobility of the process exhibited by adult specimens make it difficult to accept Heegaard's suggestion (1947:77-78) that the sternal furca is a cuticular spine.

The sternal furca of the fourth chalimus is visible developing underneath the third chalimus cuticle (Fig. 18a). The process is indistinctly visible between and slightly posterior to the bases of the maxillipeds but does not project from the ventral surface. The proximal end is broadly rounded, the bifurcation extends less than one-half of the total length of the process, and the tines are sharply pointed.

After the moult into the fourth chalimus, the sternal furca (Fig. 18b) is distinct, projecting from the ventral surface of the cephalothorax. The greatest width of the process is approximately two-thirds of the greatest length. The bifurcation extends slightly more than two-thirds of the length of the process. The tines are angled outward slightly and are bluntly rounded distally.

The sternal furca of the fifth chalimus (Fig. 18c) is well developed. The bifurcation of the process extends about one-half the length of the process. The tines appear distinct, separated from the base of the process by a groove; they are also angled outwards slightly and are bluntly pointed.

The tines of the sternal furca of the sixth chalimus do not appear distinct from the base as in the preceding stage. The bifurcation extends slightly more than one-half the length of the process; the tines are angled outward slightly and are bluntly pointed.

The sternal furca of the adult male and female (Fig. 18e) is more heavily developed than in the preceding stages. The tines have a flat inner surface in contrast to the round inner surface of the previous stages but are still angled outwards slightly and have a blunt tip.

Thoracic Leg I

The armature and character of the membranes, spines, and setae comprising the armature, are given in Table 2.

The first thoracic leg is present in the copepodite. The appendage (Fig. 18f) is biramous; the protopodite, exopodite, and endopodite are each one-segmented. The protopodite is wider distally than proximally, its greatest width slightly more than the greatest length; a single lightly plumose seta is present just lateral to the base of the exopodite and an indistinct, seta-like process is present on the proximal inner margin. The exopodite is palm-shaped, its lateral and distal margins continuous. The outer margin of the exopodite segment bears four spines, the proximal three of which are simple, the fourth with a membrane along the outer margin. The endopodite is also palm-shaped, the lateral and distal margins again continuous. The outer distal surface bears a small, triangular, spinelike projection in addition to the setae shown in Table 2.

The distinct shape of the copepodite first thoracic leg is lost in the moult from the copepodite into the first chalimus. The first thoracic leg of the first chalimus (Fig. 18g) appears flabby, the armature seems to have degenerated, and the long plumose setae borne by the exopodite and endopodite of the copepodite first leg, and presumably used in swimming, are lost and replaced by short, lightly plumose setae. The protopodite is one-segmented, its width and length about equal; the distal end is somewhat narrower than the proximal although this is variable in different specimens. A single lightly plumose seta is present on the distal lateral surface just lateral to the base of the exopodite, and the seta-like process of the preceding stage is absent. The exopodite is one-segmented and dactyliform, the proximal end is wider distally than proximally, and the greatest length is approximately $2\frac{1}{2}$ times the greatest width. The lateral margins of the segment are slightly irregular, the distal margin broadly curved. A lightly plumose seta is present on the middle of the outer lateral surface and six lightly plumose setae are present on the distal end. The spines present on the exopodite segment of the copepodite appendage are completely absent in the first chalimus. The endopodite is one-segmented and irregularly lobate, its length slightly less than two-thirds that of the exopodite. The endopodite bears two lightly plumose setae on its distal surface.

Two distinct trends can be noticed in the

TABLE 2
ARMATURE OF FIRST THORACIC LEGS OF DEVELOPMENTAL STAGES*

STAGE	MARGIN	PROTOPODITE	EXOPODITE		ENDOPODITE
			1	2	
Copepodite	outer	1s	3h,1Hm		
	inner	1P'	3P,1Q		7P
Chalimus I	outer	1p	1p,3P		1P
	inner		3P		1P
Chalimus II	outer	1p	1P,3P		1P
	inner		4P		1P
Chalimus III	outer	1p	1rh	3H	1rh?
	inner	1p		3P,1P	?
Chalimus IV	outer	1p	1rh	3H	1rh?
	inner	1p		3P,1P	1rh?
Chalimus V	outer	1p	1rh	3H	1rh?
	inner	1p	c	3P,1P	1rh?
Chalimus VI	outer	1p	1rh	3H	1rh?
	inner	1p	c	3P,1P	1rh?
Adult	outer	1p	1rh	3H,1P	?
	inner	1p	c	3P	?

* For explanation of symbols see Fig. 1.

gradual change of the first thoracic leg from the first chalimus stage to the adult. There is a gradual reduction in the size of the endopodite, with regard to the exopodite. Both the exopodite and the endopodite are of approximately equal size in the copepodite but even in the first chalimus the endopodite is distinctly smaller than the exopodite, a change that is carried through later development until in the adult the endopodite is a mere rudiment, vastly smaller than the exopodite. The second trend is the gradual elongation of the exopodite segment from the palm-shaped copepodite segment to the elongate second chalimus segment (Fig. 18*b*), then the division of this segment into two segments in the third chalimus (Fig. 18*i*) and the later elongation of each of the two segments, especially the proximal, to the adult condition (Fig. 18*m*).

The armature of the first thoracic leg changes in character more than in quantity from the first chalimus to the adult. The second chalimus exopodite bears seven lightly plumose setae on the distal surface and one short, lightly plumose seta from the middle of the outer lateral surface. The exopodite of the third chalimus, a two-segmented structure, bears three spines and one lightly plumose seta on the distal surface and three lightly plumose setae on the inner lateral surface of the second or distalmost segment in

addition to a single, spinelike process on the outer distal lateral corner of the first segment. The total number of processes on both of the segments is the same as the number on the single exopodite segment of the second chalimus although the character is quite different. The armature of the exopodite remains the same as that of the third chalimus throughout development except for the addition of a row of setules along the inner surface of the first segment. The two lightly plumose setules on the distal surface of the endopodite segment of the first chalimus are found through most of the development (see Table 2) although distinctly reduced in size until in the adult they appear as minute, indistinct projections from the distal surface of the rudimentary endopodite. One other change occurs in the armature of the first thoracic leg, the addition of a small, lightly plumose setule on the proximal inner margin of the protopodite segment of the third chalimus.

Some change occurs in the shape of the first thoracic leg segments but these are of a rather minor nature and are shown in Figure 18*f-m*.

Thoracic Leg II

The armature and character of the membranes, spines, and setae comprising the armature are given in Table 3.

The second thoracic leg is first present in the copepodite stage. As with the first thoracic leg, the appendage appears to degenerate in the first few chalimus stages and then gradually takes on the appearance of the adult appendage in the late chalimus.

The second thoracic leg of the copepodite (Fig. 19*a*), as in all of the remaining stages, is biramous. The protopodite is one-segmented, the width of the proximal and distal ends being about equal and the greatest length about three-fourths of the width. The lateral margins of the segment are broadly convex, and the distal margin is irregular. A single lightly plumose seta is present on the protopodite just lateral to the exopodite base. The exopodite is one-segmented and ovoid, and the distal margin is distinct from the outer lateral margin but is continuous with the inner. The proximal end of the exopodite is minutely bilobed and heavily sclerotized, forming an articulation surface that is contiguous with irregularities on the lateral distal surface of the protopodite. The outer surface of the exopodite bears three spines, the proximal two of which are simple, the distal long and fringed by a membrane along its outer margin. The

endopodite is one-segmented, the proximal end narrow and the distal end broad; the distal two-thirds of the segment is bent inwards. The lateral and distal margins of the segment are both distinct. Both the exopodite and endopodite bear several plumose setae as indicated in Table 3.

The second thoracic leg of the first chalimus (Fig. 19*b*) is much more simple than the copepodite appendage. The protopodite is one-segmented, and its greatest length is approximately two-thirds of its greatest width. Both of the lateral margins are continuous with the distal margin although the entire outline of the segment is somewhat irregular. The single seta present on the copepodite protopodite is absent in this stage. The exopodite and endopodite are of approximately equal length and both are dactyliiform. The exopodite is approximately one-half as wide as long although slightly wider distally than proximally; the lateral margins are wavy, the distal broadly rounded. A single naked seta is present on the middle of the outer lateral surface and five lightly plumose setae on the distal surface. The endopodite is irregularly rounded distally; the lateral and distal margins are con-

TABLE 3
ARMATURE OF SECOND THORACIC LEGS OF DEVELOPMENTAL STAGES*

STAGE	MARGIN	STERNAL PLATE	PROTOPODITE		EXOPODITE			ENDOPODITE		
			1	2	1	2	3	1	2	3
Copepodite	outer		1p		2h,1Hm					
	inner				3P,1Q			6P		
Chalimus I	outer				1p',3P			2P		
	inner				2P			2P		
Chalimus II	outer				2P,2P			2P		
	inner				4P			1P,3P		
Chalimus III	outer			1p	f,1H	4H,3P		c	c,2P	
	inner		1P	f,1s	c	c,2P		1P	4P	
Chalimus IV	outer			1p	f,1H	3H,1Q,2P			2P,2P	
		f								
	inner		1P	f,1s	c,1P	c,3P		1P	3P	
Chalimus V	outer			1p	f,1H	3H,1Q,2P		c,C	c,1P,3P	
		f								
	inner		1P	f,1s	c,1P	c,3P		1P	c,3P,2P	
Chalimus VI	outer		1s	1p	f,1H	1H	2H,1Q,3P	c,C	c	c,3P
		f								
	inner		1P	f,1s	c,1P	c,1P	c,2P	1P	c,2P	3P
Adult	outer			f,1p	f,1H	1H	2H,1Q,2P	c,C	c	c,3P
		f								
	inner		1s,1P	f,1s	c,1P	c,1P	c,3P	1P	c,2P	c,3P

* For explanation of symbols see Fig. 1.

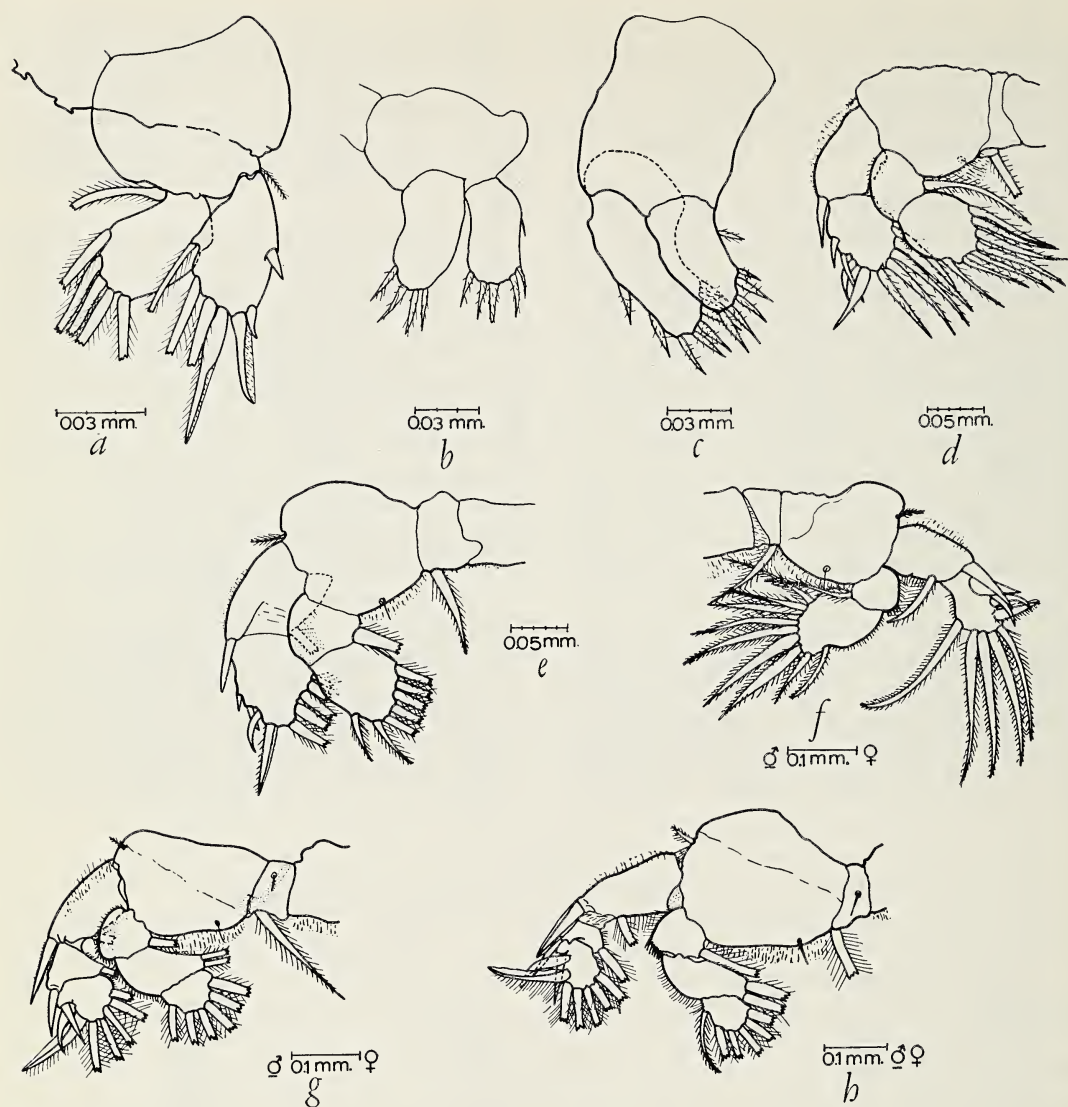


FIG. 19. Second thoracic legs of developmental stages of *L. dissimulatus*. a, Copepodite; b, first chalimus; c, second chalimus; d, third chalimus; e, fourth chalimus; f, fifth chalimus; g, sixth chalimus; h, adult.

tinuous. The greatest width of the endopodite segment is approximately one-half of the greatest length; the distal surface bears four lightly plumose setae.

Some enlargement has occurred in the second thoracic leg of the second chalimus (Fig. 19c), especially in the protopodite. The protopodite is still one-segmented, its greatest width being approximately three-fourths of its greatest length. The proximal margin of the segment

is indistinct, and the lateral margins are almost parallel. The protopodite is approximately twice the length of the first chalimus protopodite although its width is about the same. The one-segmented, dactyliform exopodite is attached to the distal surface of the protopodite. The greatest width of the segment is approximately one-half of the greatest length; the lateral margins are irregular, the distal rounded. Two lightly plumose setae are present on the distal one-half

of the outer surface and six are borne on the distal surface. The one-segmented, dactyliform endopodite is attached to the inner distal surface of the protopodite. The greatest length of the segment is about two-thirds of the length of the exopodite, its width about one-half of its length. The endopodite is tapered slightly towards the rounded distal end which bears five lightly plumose setae; an additional lightly plumose seta is present on the middle of the inner margin.

As with the first thoracic leg, the second shows a rather distinct transition in the moult from the second chalimus to the third. The appendage in the third chalimus (Fig. 19*d*) has changed from the rather generalized condition in the second chalimus to a condition which, with some exceptions, resembles that of the adult.

The protopodite of the second thoracic leg of the third chalimus is two-segmented. The first segment is narrow and forms a strip between the sternal plate and the second segment. A single plumose seta arises from the inner surface of the first segment. The second segment is broad and flattened, its greatest width is almost three-fourths of the greatest length, the outer margin is irregular, and the inner margin is convex. The exopodite, which is attached to the outer distal surface, is two-segmented. The length of the first segment is slightly greater than that of the second, and the greatest width is approximately two-thirds of the length; the lateral margins are irregularly convex. A long spine is present on the outer distal surface and is directed distally; the length of the spine is slightly less than two-thirds of the segment length. The second segment is slightly longer than wide, and the proximal end is narrower than the distal; both of the lateral margins and the distal margin are distinct, not continuous, and are irregular; the outer lateral surface bears four spines on the distal one-half of the segment. The proximalmost of the four spines is short and directed distally and laterally; the second spine is directed in the same manner as the first but is considerably longer; the third is directed laterally, curves distally, and is about the same length as the second; the fourth or distalmost spine is directed laterally and is more strongly developed than the preceding three.

The endopodite, attached to the inner distal surface of the protopodite, is also two-segmented. The first segment is approximately two-thirds as wide as long and is curved inwards, the outer lateral margin being much longer than the inner and convexly curved. The second segment is slightly less than $1\frac{1}{2}$ times the length of the first and is longer than wide; both of the lateral margins are flatly convex and distinct from the distal margin, which is irregularly rounded. Both the exopodite and the endopodite bear setae, as indicated in Table 3.

The second thoracic leg of the fourth chalimus (Fig. 19*e*) is similar to that of the third chalimus. There has been some expansion of the protopodite segments and the first exopodite segment. The setae appear to be more plumose and, in general, the armature is more like that of the adult.

The second thoracic leg of the fifth chalimus (Fig. 19*f*) is similar to that of the preceding stage although changes have occurred in the shape and the armature. The protopodite is two-segmented, the first segment short, being approximately one-third the length of the second segment; the width of the first segment is approximately three-fourths of the length. The outer margin of the first protopodite segment is longer than the inner, the proximal margin is angled, and the distal is straight. Further, the outer proximal surface of the segment has a small knoblike projection that articulates in a C-shaped depression in the end of the sternal plate (not shown in the figure), and the inner margin bears a single plumose seta. The second segment is swollen distally, the greatest width of the distal region being approximately four-fifths of the greatest length; the outer lateral margin of the segment is irregular, the inner broadly convex. The exopodite is still two-segmented, the first segment slightly longer than the second. The outer margin of the first segment is convex, and the inner margin is slightly irregular. The outer distal corner of the first segment bears a long, distally projecting spine that extends to the distal region of the second segment. The second segment is palm-shaped, being wider distally than proximally. The greatest width of the segment is approximately two-thirds of the greatest length; the outer lateral margin is irregular and bears three strongly-

developed spines, the proximal two extending distally and laterally, the distalmost extending laterally and curving distally. The simple fourth spine of the third chalimus bore a membrane on the inner margin and a row of setules on the outer in the fourth chalimus; this condition is reversed in the fifth chalimus. The endopodite is two-segmented; the first segment is short, its width slightly greater than the length which is approximately one-half that of the second segment. Both of the lateral margins of the first segment are convex, the outer twice the length of the inner. The second segment is irregularly palm-shaped, and the lateral margins are irregular although distinct from the distal margin; the greatest width of the segment is approximately two-thirds of the greatest length.

The second thoracic leg of the sixth chalimus (Fig. 19g) is basically the same as that of the adult. The protopodite is two-segmented; the first segment is short, less than one-third of the length of the second. The second segment is broader distally than proximally, its greatest width approximately two-thirds of the length. The lateral margins of the second segment are slightly wavy, the inner generally convex. The exopodite is now three-segmented, the division occurring in the second segment of the previous stage, just distal to the proximalmost spine. The first exopodite segment is slightly longer than the combined lengths of the succeeding two segments, and its lateral margins are flatly convex. The single spine is slightly denticulated and strongly developed and extends past the distal end of the second segment. The second segment is short, flared from the narrow proximal to broad, concave distal surface. A single simple, although well-developed, spine is present on the outer distal surface. The third segment is short, its length approximately equal to that of the second segment. The distal one-half of the segment is broadly rounded and a small, steplike indentation is present in the proximal one-half of the outer margin. A well-developed, simple, distally projecting spine is present in the indentation and a second well-developed, simple spine projects laterally and curves distally from the outer lateral surface at the junction of the curved and indented margins. The endopodite is also three-segmented. The first segment is approximately equal in length to the

second; the outer margin is broadly rounded and approximately 4 times the length of the short, irregular inner margin. The second segment is flared from the narrow proximal to broad distal end, as in the second segment of the exopodite. The outer margin of the second segment is flatly convex, the inner slightly concave. The third segment is short, being approximately three-fourths of the length of the second segment. The distal and lateral surfaces are irregularly rounded, the margins continuous.

With the exception of some minor changes in the shape and armature of the segments, the description of the second thoracic leg of the sixth chalimus can be applied to the adult appendage (Fig. 19b).

Thoracic Leg III

The armature and character of the membranes, spines, and setae comprising the armature are given in Table 4.

The biramous third thoracic leg is first present as a recognizable appendage in the first chalimus (Fig. 20a). As mentioned earlier, however, two spinelike processes are present on the third pedigerous segment of the copepodite and may represent the third legs in this stage of development. The protopodite of the third thoracic leg of the first chalimus is one-segmented, its greatest width and length about equal. The somewhat irregular outer lateral margin is more than twice the length of the inner and two naked setules are present on the outer lateral surface just lateral to the exopodite base. The exopodite is one-segmented, broader than long; its lateral margins are generally convex and the distal margin is flat although variable in shape in different specimens. Four spinule-like processes project from the distal region of the exopodite. The endopodite is also one-segmented and broadly rounded, both of the lateral and the distal margins being continuous; the greatest width of the segment is slightly more than the length.

The protopodite of the third thoracic leg of the second chalimus (Fig. 20b) is much larger than that of the preceding stage, most of the increase in size being due to the increase in the lateral surface. The irregular proximal end of the one-segmented protopodite is broad, approximately twice the width of the distal end. The outer lateral margin is almost 4 times the

length of the inner. The exopodite and the endopodite differ from those of the preceding stage in shape and armature. The one-segmented exopodite is broader than long, the lateral margins are irregular although slightly convex, and the distal margin is irregularly rounded. Both the outer and inner lateral margins have several irregularly spaced setules and the distal surface bears two spinelike processes. The one-segmented endopodite is about one-half the length of the exopodite although both the length and width of the segment are approximately equal; the lateral margins are almost parallel, the distal margin slightly rounded, and the inner distal surface gives rise to two spinelike processes.

The third thoracic leg of the third chalimus (Fig. 20c) is distinctly different from that of the second chalimus. It appears that the third chalimus marks a distinct change in the first three pairs of thoracic legs. The protopodite is now broader although the added breadth appears to have been gained as a result of a lengthening of the distal margin or an inclusion of the inner lateral margin with the distal; both the exopodite and the endopodite are now two-segmented and the armature has changed.

The protopodite of the third thoracic leg of the third chalimus is broad and flattened. The greatest width, across the proximal end, is

slightly less than twice the length; the inner lateral margin appears to be incorporated into the distal margin although distinct evidence of this is lacking. A single plumose seta is present just lateral to the junction of the protopodite and sternal plate. The exopodite, attached to the lateral region of the distal protopodite surface, is two-segmented, the first segment slightly shorter than the second; the outer margin of the first segment is convex, the distal margin sloping to the proximal margin in older specimens but not distinctly so in younger specimens. The second segment is as wide as long, the lateral margins are irregular, the distal margin is rounded, and the surface bears three lightly plumose setae. The endopodite is two-segmented although the division between the first segment and the protopodite is indistinct in older specimens. The outer margin of the first segment is longer than the inner, and the proximal and distal margins are irregular. The second segment is approximately equal to the greatest length of the first segment and is almost circular in outline.

The protopodite of the third thoracic leg of the fourth chalimus (Fig. 20d) is broader than that of the third and the length has also increased so that the greatest proximal width is only about three-fourths of the greatest length.

TABLE 4
ARMATURE OF THIRD THORACIC LEGS OF DEVELOPMENTAL STAGES*

STAGE	MARGIN	STERNAL PLATE	PROTOPODITE	EXOPODITE			ENDOPODITE	
				1	2	3	1	2
Chalimus I	outer		2p'	2h				
Chalimus II	inner			2h				
	outer			c,2h				
Chalimus III	inner			c			2h	
	outer		1p		3P			2P
Chalimus IV	inner		1P,f				1P	1P
	outer		1p		3P			1p,2P
Chalimus V	inner		1P,f				1P	1P
	outer		f,1P		c,4p'		c	c,2P
Chalimus VI		f						
	inner		1P,f	1p,1H'	5P		1P	2P
Chalimus VI	outer		f,1P		c,1p'	c,3p',1P	c	c,1p,3P
		f						
Adult	inner		1P,f,2s	1H'	1P	3P	1P	2P
	outer		f,1P		c,1p'	c,3p',1P	c	c
Adult		f						
	inner		1P,f,2s	1H'	c,1P	c,3P	1P	c,5P

* For explanation of symbols see Fig. 1.

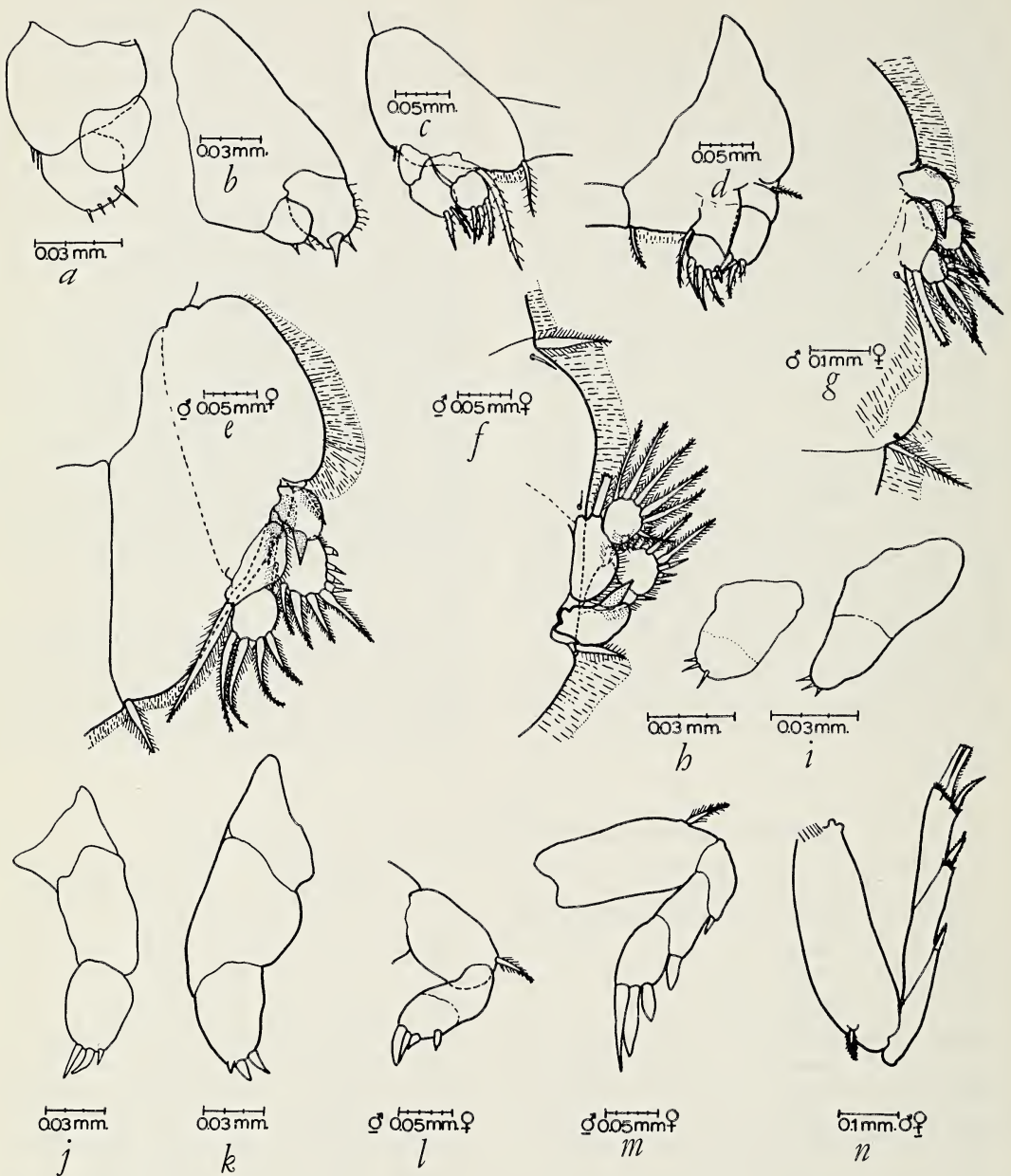


FIG. 20. Third and fourth thoracic legs of developmental stages of *L. dissimulatus*. *a-g*, Third thoracic legs: *a*, First chalimus; *b*, second chalimus; *c*, third chalimus; *d*, fourth chalimus; *e*, fifth chalimus; *f*, sixth chalimus; *g*, adult. *b-n*, Fourth thoracic legs: *b*, First chalimus; *i*, second chalimus; *j*, third chalimus; *k*, fourth chalimus; *l*, fifth chalimus; *m*, sixth chalimus; *n*, adult.

The protopodite tapers distally, the lateral margins are slightly irregular, and the distal margin is continuous with the outer lateral margin. The exopodite is two-segmented, the second segment $2\frac{1}{2}$ times the length of the first. The base of the spine-bearing first segment of the fifth chalimus is visible inside the first segment of the fourth chalimus; the lateral margins of the fourth chalimus segment are convex. The spine-bearing segment mentioned above and present in the fifth and sixth chalimus in addition to the adult replaces the first segment of the third and fourth chalimus; the second segment of these two stages remains as the second segment, which later divides to form the second and third segments. The lateral and distal margins of the second exopodite segment of the fourth chalimus are continuous, the distal end is broadly rounded, and the surface gives rise to three lightly plumose setae. The endopodite is two-segmented although the division between the first segment and protopodite is indistinct and incomplete. The second segment is as wide as long and has a broadly rounded outline with the lateral and distal margins being continuous. The distal surface of the segment bears four lightly plumose setae.

The third thoracic leg of the fifth chalimus stage (Fig. 20e) possesses characteristics very similar to those of the adult. The protopodite is one-segmented and greatly expanded from the previous stage. The sternal plate, connecting the protopodites of the two legs, is broad and forms a laminate projection from the posterior ventral surface of the cephalothorax. The exopodite is still two-segmented, the first segment possessing a strongly-developed, spinelike projection from the inner distal surface. The proximal end of the first segment is distinct from the protopodite ventrally although it is still fused dorsally to the protopodite and the distal end to the second segment. The first segment, other than the process, is short, the width being greater than the length. The second segment is broadly rounded, the lateral margins continuous with the distal. The proximal end of the segment is narrow and the segment appears palm-shaped; the greatest width is slightly more than two-thirds of the length. The endopodite is two-segmented; the first segment is twice as wide as long and appears as a narrow band with a swollen outer

lateral region. The second segment is attached to the inner distal surface of the first and is broadly rounded, the lateral and distal margins being continuous. The greatest length of the second segment is slightly greater than that of the first; the width and length are, however, approximately equal.

With minor exceptions, the third thoracic leg of the sixth chalimus (Fig. 20f) and the adult (Fig. 20g) are the same. The protopodite of the sixth chalimus is broadly flattened and laminate; the lateral and distal margins are continuous. The exopodite is now three-segmented, the first segment forming the base for a strongly developed, spinelike process that projects from the distal inner margin as in the preceding stage. The lateral margins of the first segment are irregular, the outer being generally convex and the inner almost straight. The second segment is short and flared from the narrow proximal to broad, concave distal end. The third segment is also short, being approximately equal in length to the second, and the width is slightly greater than the length; the lateral margins of the segment are rounded and continuous with the rounded distal margin. The endopodite is two-segmented, the first segment broad, its width approximately $1\frac{1}{2}$ times its length. The outer two-thirds of the distal margin of the first segment is convex, the inner one-third concave; the outer lateral margin is continuous with the distal margin, and the inner margin is irregular. The second segment is slightly shorter than the first segment and is attached to the concave inner distal surface of the first. Both of the lateral margins are continuous with the distal margin in the second segment.

The protopodite of the adult third thoracic leg (Fig. 20g) is broader than that of the sixth chalimus; the first endopodite segment is slightly longer, although not wider, and the armature of the appendage has changed slightly in the moult from the sixth chalimus to the adult. Other than these differences, the appendages of the two stages are the same.

Thoracic Leg IV

The armature and character of the membranes, spines, and setae comprising the armature are given in Table 5.

The uniramous fourth thoracic leg is first

present in the first chalimus (Fig. 20*b*). The appendage in this stage is a one-segmented lobe. The proximal end is broader than the rounded distal end, the lateral margins are wavy, and the distal surface bears three spinule-like processes.

The fourth thoracic leg of the second chalimus (Fig. 20*i*) is lobate and somewhat longer than the appendage of the preceding stage. An indistinct division is present in the middle of the appendage, dividing it into two segments. Whether it is right to call the proximal segment of the appendage the protopodite and the remaining segments the exopodite as this author has previously done with regard to adult caligids (Lewis, in press) was not determined. For the present, however, because of the lack of definite information on this problem, the terms "protopodite" and "exopodite" will not be used but the segments simply referred to by number, with the proximalmost segment being the first. The proximal end of the first segment of the fourth thoracic leg of the second chalimus is broad and angled so that the appendage projects posteriorly and laterally from its junction with the fourth pedigerous segment. The second segment bears three short, terminal, spinelike processes.

The fourth thoracic leg of the third chalimus (Fig. 20*j*) has lost its general lobate shape and is now three-segmented. The first segment is short, its greatest length approximately three-fourths of the width; the segment is tapered from the broad proximal to somewhat narrower distal end. The second segment is about twice the length of the first and almost twice as long

as broad; the lateral margins are irregular although basically parallel, and the distal and proximal margins are both irregular. The third segment is greater than one-half the length of the second, the lateral margins are flatly convex, and the distal margin is rounded and continuous with the inner lateral margin. Three spinelike processes are present on the distal surface of the third segment.

The fourth thoracic leg of the fourth chalimus (Fig. 20*k*) is somewhat similar to the third chalimus appendage. The length and width of the entire appendage is slightly greater than that of the preceding stage, the first segment is comparatively shorter and wider, the second segment appears swollen, and the third segment is not as distinctly separated from the second.

The fourth thoracic leg of the fifth chalimus (Fig. 20*l*) is three-segmented. The first segment is ovoid, the lateral and distal margins broadly rounded and the outer distal lateral surface bearing a single plumose setule. The division between the second and third segments is indistinct in contrast to the distinct division present in the preceding stage. The combined lengths of the second and third segments is approximately equal to that of the first segment. One poorly developed spine is present on the outer distal lateral surface and two well-developed and one poorly developed spines are borne on the distal surface of the third segment.

The fourth thoracic leg of the sixth chalimus (Fig. 20*m*) is four-segmented. The first segment is slightly longer than the combined lengths of the three distal segments, the proximal and distal ends of the segment are slightly narrower than the middle of the segment, and the lateral margins are wavy. A single plumose setule is present on the outer distal lateral surface of the segment, as in the preceding stage. The second segment is short, its greatest length slightly less than that of the third segment; the lateral margins are flatly convex, the outer much longer than the inner. A short, simple spine is present on the outer distal corner of the second segment. The third segment is tapered from the proximal to slightly broader distal end; the lateral margins are flat or flatly convex, the outer longer than the inner. A single simple spine is present on the outer distal corner of the segment. The fourth segment is slightly broader

TABLE 5
ARMATURE OF FOURTH THORACIC LEGS OF
DEVELOPMENTAL STAGES*

STAGE	MARGIN	SEGMENTS			
		1	2	3	4
Chalimus I	outer	3h			
Chalimus II	outer		3h		
Chalimus III	outer			1h,2H	
Chalimus IV	outer			1h,2H	
Chalimus V	outer	1p		1h,1h,2H	
Chalimus VI	outer	1p	1h	1H	3H
Adult	outer	1p	1H	1H	3H

* For explanation of symbols see Fig. 1.

TABLE 6
MEAN LENGTH OF ATTACHMENT FILAMENT

	COPEPODITE	CHALIMUS					
		1	2	3	4	5	6
Measurement (in mm)	0.136	0.111	0.146	0.156	0.155	0.163	0.213
Number of specimens	1	6	30	13	60	7	2

distally than proximally; the lateral margins are flatly convex, the distal surface almost flat and bearing three simple although well-developed spines. The innermost of the three terminal spines is longest, the outermost shortest.

The make-up of the fourth thoracic leg of the sixth chalimus is similar to that of the adult (Fig. 20*n*) although the armature is more simple. The segments of the adult, particularly the distal three, are more elongate; the terminal spines on each segment have at least one denticulated or frilled margin and are encircled by a frilled process at their base.

Caudal Rami

The caudal rami are first present in the copepodite stage (Fig. 12*a*). These structures, in the copepodite, are slightly more than one-half of the greatest length of the combined genital segment and abdomen and their greatest width is approximately equal to the length. Both of the lateral and the distal margins are irregular. Two short, plumose setae are present on the proximal one-half of the outer lateral surface and two long, plumose setae arise from the distal surface.

The caudal rami of the first chalimus (Fig. 12*b*) arise from the posterior ventral surface of the genital-abdominal segment. The greatest length of the rami is approximately two-thirds of the width; the lateral and distal margins are continuous. Six plumose setae are present on the rami, two on the distal lateral surface, three on the distal surface, and one on the inner distal corner.

The caudal rami of the remaining chalimus stages and the adult (Fig. 12*c-l*) are similar in shape and make-up to the rami of the first chalimus. Minor differences such as the setulation of the inner margin in the second chalimus (Fig. 12*c*) and succeeding stages and a variation in the length of the setae are the only sig-

nificant changes that occur after the first chalimus.

REMARKS ON BEHAVIOR OF DEVELOPMENTAL STAGES AND THEIR RELATION TO HOST

Both of the planktonic first and second naupliar stages exhibit a strongly positive phototropism in the laboratory. Movement in both of these stages is sporadic and jerky, the three pairs of appendages present on each of these stages moving in unison in a series of strokes and then remaining motionless for a short period of time. The animal thus makes a short but swift movement and then rests, sinking gradually. Whether it is the response to light or a more intrinsic factor that controls the amount of time spent in swimming and in resting was not determined. The function of the balancers present on the posterior end of the nauplii has been suggested to be the balancing of the nauplius when it is at rest (Wilson, 1905:538). Since these structures were not seen to move to any extent in *L. dissimulatus*, their function cannot be definitely ascertained although their structure and position do suggest that they play a role in the positioning of the nauplius during both movement and rest.

As the age of the second nauplius increases, the positive reaction to light decreases, a condition that extends into the planktonic phase of the copepodite. A light placed on one side of a finger bowl caused some copepodites to swim towards that side. The tendency, however, was not as great as in the naupliar stages and appeared to diminish as the age of the copepodites increased. The movement of the copepodite was quite rapid although jerky and irregular; the periods of time spent in swimming were longer, and the time spent in resting shorter than in either of the two naupliar stages. During the resting phase the copepodite appeared to sink

faster than did the nauplius, which can be explained by the apparent increase in body volume and the decrease in relative number and length of setae. Copepodites were kept up to 72 hours in culture. After about 10 hr they began to prod the bottom and sides of the dish with the anterior end of their body. Inasmuch as the copepodite is the attachment stage, the prodding may have some relation to the attachment of the animal to its host.

As was mentioned earlier, attachment was observed in only one copepodite. Attachment was accomplished by hooking the strong, claw-like terminal processes of each second antenna into the substrate. The formation of the attachment filament was not seen in the single copepodite that attached in the laboratory. To determine the means by which the filament was formed, several copepodites were collected that had attached to the host and formed a filament. These animals were separated from the host by severing the filament close to the body of the copepodite. A piece of loosely woven nylon cloth was then placed in a finger bowl and the detached copepodites placed in with it. Those specimens that reattached did so by holding themselves to the cloth substrate by means of their maxillipeds and second antennae. They then placed their body at an angle to the substrate, with the anterior end in close proximity to it, and, by jabbing the substrate with the middle of the frontal region, they appeared to secure either the remaining attachment filament or a new filament formed by a secretion that hardened almost immediately on the substrate as an irregular lobe, not the disk found in copepodite and chalimus specimens normally attached to the host. After the filament was attached, the terminal processes of the maxillae were used to stroke the filament between the frontal region and the substrate while the copepodite backed off from the point of attachment. The backing off of the animal appeared to cause the material secreted by the frontal organ, either before or after the animal started backing off, to be drawn out into a filament and the stroking by the maxillae to make the filament more even.

After the attachment, the activity of the copepodite decreased. This observed lower activity rate was noted for the first four chalimus stages

although activity did increase to some extent during the actual shedding of the old cuticle in moulting.

Heegaard (1947:90-94) indicates that the various attached stages of *Caligus curtus* secrete the attachment filament anew each time a moult occurs. During the period of moulting observed in both copepodite and chalimus stages in *L. dissimulatus*, the original filament remained attached to the animal, the cuticle rupturing on the anterior dorsal surface and the animal, by vigorous movements of its body, freeing itself from the old cuticle and passing it posteriorly over the posterior end of the body. The shed cuticle did not remain attached to the host or to the frontal filament. Heegaard (1947: fig. 32) figures a portion of the fin ray of a cod with several attachment filaments of *Caligus curtus* hanging from it and (1947:92) suggests that these are left by the various chalimus stages. The only attachment filaments that were observed in host tissue and could be definitely tied in with a chalimus were those from specimens of the fifth and sixth chalimus stages of *L. dissimulatus* that had just broken free and assumed the free-moving adult type of existence.

Gurney (1934:184, 186, 188) indicates that the attachment filament is increased in length slightly at each moult as indicated by the small annuli at the proximal end of the attachment filament of later chalimus larvae. This could not be verified or disproved for *L. dissimulatus*, as the attachment filament is irregular at the proximal end at all stages of development, from the copepodite to specimens of the sixth chalimus that are still attached. The mean length of the filament during each stage is given below in Table 6 and suggests that a small amount of new material is added although the lack of specimens in some of the stages does not provide substantial proof of this.

Shiino (1959:305) reports chalimus larvae and young stages of *L. dissimulatus* from the gills of *Bodianus diplotaenia* captured in the Revilla Gigedos Islands and includes several figures of these stages. This report is of interest because of the place of attachment of the chalimus larvae. With only two exceptions, all of the chalimus larvae of Hawaiian specimens of *L. dissimulatus* were found attached to the upper surface of the buccal cavity of the host. The

two exceptions were chalimus larvae found attached to the gill membrane of *Acanthurus triostegus sandwicensis*. The number of larvae present in the buccal cavity of infected fishes ranged from 1 to 203. In the specimen of *Acanthurus olivaceus* possessing 203 attached copepodites and chalimus larvae, the roof of the mouth appeared to be actually shingled with copepods.

After breaking free from the attachment filament, the fifth or sixth chalimus moves out of the buccal cavity either into the gill cavity or onto the external surface. The final moult, from the sixth chalimus to the adult, is accomplished outside of the buccal cavity. Only one observation of the final moult was made and this was after the adult had broken through a split in the anterior dorsal surface of the sixth chalimus cuticle. At the beginning of the observation the animal had pulled the second antennae free from the old cuticle and was not actively moving, holding on to the host by means of the maxillipeds and keeping the second antennae free. After a short period of time the second antennae were used to grasp the surface and the maxillipeds and remaining appendages were pulled free from the cuticle. By means of violent wriggling of the body and appendages, the cuticle was shed over the posterior end of the body. After a second short period of time, during which the newly emerged adult remained attached by the second antennae, all of the thoracic appendages and the maxillae were moved randomly and the animal then assumed the adult role of skittering over the surface of the host.

Fertilization occurs just after the terminal moult. The male at this stage of development is almost completely grown; the female is still small and will increase in size in the adult stage. The actual placement of the spermatophores, held within the genital segment of the male, was not observed. Several mating pairs were collected and observed, however. The male was found to clasp the fourth pedigerous segment or the anterior end of the genital segment of the female with the second antennae. The function of the maxillipeds in mating was not determined, although in all observed pairs the maxillipeds of the male were free. A. Scott (1901:28) and Wilson (1905:528) indicate that the caligid spermatophore is viscid and, as noted for *L. dissimulatus*, that it forms an

oval or tear-shaped body in the posterior region of the genital segment. The male presumably bends the posterior region of its body, the free segments, underneath itself and, upon contact with the posterior ventral surface of the female, discharges the two spermatophores which adhere to the genital segment of the female. No remating was observed and, as suggested by Wilson (1905:527), the single mating just after both sexes moult into the adult probably suffices for the entire egg production of the female.

The young adult female was found in both the gill cavities and on the external surface of the body. Large females carrying egg strings were found primarily in the gill cavity. The copepod appears to have more protection in the gill cavity, especially against being swept off of the host by water currents or brushed off when the host comes in contact with the substrate. The position of the female on the host thus may be dependant upon its size and upon the presence or absence of egg strings which, it appears, add a considerable burden.

The duration of the adult life is not known. Females kept in the laboratory produced up to three sets of egg strings, each string being extruded approximately 21 hr after the previous string had hatched. Thirty to 40 hr is the average interval between extrusion of the eggs and hatching. The period of time between fertilization and the production of the first pair of egg strings is not known, neither is the time from moulting into the adult until the female is fertilized. Further, the conditions provided in the laboratory were far from those in the natural environment and it is felt that the number of egg string sets produced is probably more than the three obtained in the laboratory.

SUMMARY

1. The external anatomy of the 10 stages in the life history of *Lepeophtheirus dissimulatus* is described and figured.

2. The general behavior of the various stages is discussed. The first two, the naupliar stages, are planktonic. The third or copepodite stage is planktonic early in its existence but later attaches to the fish host by means of the prehensile second antennae. After attachment, the copepodite secretes a frontal filament that is em-

bedded in the tissue of the host and enables the copepodite and following attached larval stages to remain attached to the host without using their appendages. At least four of the six chalimus stages that follow the copepodite remain attached to the host by the frontal filament; the fifth and sixth chalimus stages may either be found attached or free on the host. The adult is found moving freely over the surface of the host.

ACKNOWLEDGMENTS

Part of this study was aided by a grant from the Sigma Xi-RESA Research Fund, 1961. The author is grateful to Samuel Kaolulo and to Lester Zukeran for host material. He also wishes to express his appreciation to the members of his thesis committee for their counseling and guidance during the preparation of his thesis, which included the life history of *L. dissimulatus*.

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Studies on the Green Alga, *Udotea indica* A. & E. S. Gepp, 1911

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ABSTRACT: In *Udotea indica* reproductive organs are terminal and club-shaped. Numerous biflagellate zooids are produced in the reproductive organs. *Udotea* is named as the type of a new family, Udoteaceae.

Udotea indica A. & E. S. Gepp (1911) was first collected by J. A. Murray (in 1880–83) from Karachi near the mouth of the Indus River. The type specimen is in the British Museum and the type locality is Karachi. Previous taxonomic studies have been made, notably by Boergesen (1930, 1934) and Taylor (1950). This species has also been reported from Bikini and other areas in the Marshall Islands by Taylor (1950). It grows in association with *Chaetomorpha* sp. on silt-covered rocks along the edges of littoral rocky pools, where it generally occurs in patches, but elsewhere it may be found scattered on rocky platforms.

The genus has been included in the family Codiaceae by previous authors. The present study excludes *Udotea* from the Codiaceae and places it in a family of its own. The basis for this conclusion is that in *Udotea indica* the terminal portions of the filaments are transformed into reproductive organs, in contrast to the lateral position of the reproductive organs in the genera of the family Codiaceae.

The discovery, made while examining living material, that the reproductive bodies are motile made a thorough investigation of this *Udotea* necessary. The present account gives the preliminary results of this study and, while not completely clarifying many features, shows that *U. indica* is not a member of the Codiaceae. The structure and reproduction of this species are discussed below.

The thalli are up to 4 cm long, as much broad, and are slightly calcified. The root-mass forms a small tuft. The terete stipe is up to 1.2 cm

long and 1 mm thick. The fronds are green, somewhat rounded, flabellate, orbicular, and sometimes broadly proliferated above; the base is cuneate, distinctly zonate. The blade margins are entire, lobed, or lacerated.

Filaments 31–48 μ in diameter, radiating from the stipe to the margin, slightly parallel or interdigitated, pluriseriate to triseriate, dichotomously branched, supra-dichotomal constriction uneven. The filaments possess numerous unilateral or bilateral, short or pedicellate or truncate appendages that are simple or lobed. The appendages are so fitted together as to form a primitive cortex. The filaments of stipes are irregularly dichotomously branched, having lateral appendages (Fig. 1a-e). Reproductive organs formed terminally on the filament (Fig. 1d, e), each with a thick constriction in the middle, up to 16.2 mm long and 2.4 mm broad.

The present effort is the first study made of reproduction in *Udotea*. The previous report on the presence of reproductive organs was considered erroneous by Ernst (1904) and Fritsch (1956), who supposed the structures reported as reproductive to be epiphytes.

The filaments are compact and interdigitated; but when fruiting occurs the terminal parts swell and separate, and cytoplasm passes into the swollen parts, forming reproductive organs. The lower part of each serves as a stalk of the reproductive organ (Fig. 1e). The terminal portion of the fertile frond becomes loose, and as the filaments separate the reproductive organs show (Fig. 2); but in vegetative fronds the terminal edge of a blade is compact.

Numerous zooids are produced and they are liberated successively through an apical pore. On liberation of the zooids the middle constrict-

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FIG. 1. *Udotea indica*. *a*, Lower part of a filament; *b*, middle part of a filament; *c*, upper part of a filament; *d*, upper part of a filament, showing reproductive organ; *e*, upper part of a filament, showing mature reproductive organ.

tion relaxes, increasing in diameter, and thus making way for the contents from the basal part to stream into the terminal part of the reproductive organ. This process is continued until all the zooids are extruded. These zooids seem to be morphologically similar. Fusion between them has not been observed. Their study is still in progress.

In *Codium* and *Halimeda* special lateral gametangia are formed, whereas in *Udotea indica* terminal reproductive organs are formed. Such terminal club-shaped sporangium formation has been observed (Howe, 1907) on blades of *Avrainvillea*. This transformation of the terminal parts of the filaments into reproductive organs clearly distinguishes these genera from other members of the family Codiaceae.

The filaments of *Udotea indica* resemble those of *Codium* and *Halimeda* in their siphonaceous and dichotomous character, but differ in possessing uni- or bi-lateral appendages. The filaments in *Avrainvillea* are moniliform in appearance, due to the numerous constrictions, but whereas

appendages are found in *Udotea* there are none in *Avrainvillea*.

Udotea certainly represents a distinctive family, which I here name the Udoteaceae, but the systematic position of this family must await more complete knowledge of its members' life histories.

Udoteaceae fam. nov.

Frond flabellate, orbicular, broadly proliferated above. The base cuneate, distinctly zonate, margin entire, lobed, or lacerated. Filaments radiating from stipe to the margin, slightly parallel or interdigitated, pluriseriate to triseriate, dichotomously branched, supra-dichotomal constriction uneven, uni- or bi-lateral short pedicellate or truncate appendages simple or lobed. Appendages so fitted together as to form a primitive cortex. Terminally formed reproductive organ with a thick constriction.

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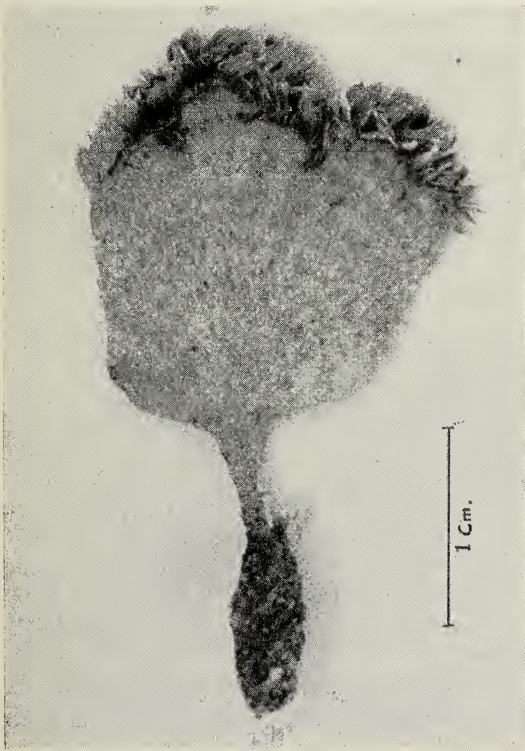


FIG. 2. Fertile plant.

Effects of Pollution on the Amino Acid Content of *Mytilus edulis*

RITA D. SCHAFER¹

ABSTRACT: In an attempt to determine the influence of polluted water on the amino acid content of *Mytilus edulis*, muscle tissue of specimens from a clean area was compared with that of specimens from polluted areas and with that of specimens transferred from clean to polluted water. Analyses were made by means of two-dimensional paper chromatography. The amino acids present under one type of environmental condition but not under another were cystine, cysteine, methionine, taurine/asparagine, and proline.

It has long been known that marine waters containing pollutants affect in various ways the fauna inhabiting such waters. A number of studies have shown that pollution factors aid the settlement and growth of some species while inhibiting others. Wilhelmi (1916) points out that some species are so favored by such an area that they occur in numbers sufficient to permit them to be considered as pollutant indicators. Reish (1955, 1956, 1957a, 1957b) calls attention to the presence of *Capitella capitata* in all areas of pollution in southern California; and in a later study (1960), in which he classifies areas as to degree of pollution, he points out that each type of area is characterized by the presence of dominant species of polychaetes. Hartman (1950) states that near a disposal outfall in Santa Monica Bay, California, only two major groups of animals are present, the annelids and the crustaceans. Filice (1959) in discussing the distribution of bottom fauna in polluted estuarine waters, states that the occurrence of some species as well as their concentrations will vary with the nature and degree of pollution. Blevgad (1932), investigating effects of pollution on bottom fauna, found "dead" areas at the point of sewage outfalls. He points out, however, that at a distance slightly over 100 m away, conditions are the same as at a greater distance.

McNulty (1957), in a study of the effects of pollution in Biscayne Bay adjacent to the Miami shoreline, indicates that pollution in some instances has had a beneficial effect on productivity of macroorganisms. Hartman (1960), summarizing the results of extensive selected sampling of 11 southern California coastal areas, states that productivity and variation of organisms differ according to types of sediments, depth of bottom, availability of food, and effects of waste discharges. She also noted that biomass values are lowest in shallow depths of Santa Monica Bay, an area into which the largest of the Los Angeles disposal plants empties. The biomass values of this region were comparable to those from oily samples taken in a more northern area. In addition to these variations in ability to survive and, in some cases, to thrive in waters containing pollutants, it has been noted that the biochemical composition of some forms living in such an environment differs from that of the same species from clean waters (Schaffer, 1961). Forms previously used for investigation were the abalone, *Haliotis cracherodii*, and the crab, *Pachygrapsus crassipes*. In these the free amino acids present in specimens from polluted areas were compared with those from nonpolluted areas.

It is the purpose of the present study not only to evaluate the differences in amino acids in another organism from clean and polluted areas, but to investigate as well the effect upon

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the free amino acids of transfer from a clean area to a polluted one.

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MATERIALS AND METHODS

In the present study the wharf mussel, *Mytilus edulis*, was selected for investigation. Its wide occurrence made it easily available from a variety of areas of varying environmental conditions. Because of its sessile nature and presence on floats, it was possible to use specimens which had been constantly subjected to the conditions prevailing in the area from which it was taken. No attempt was made to differentiate sexes or size of specimens, as preliminary tests showed no amino acid differences in these respects in this species.

Comparisons of free amino acids were made on muscle tissue of animals from (1) different polluted areas, (2) an area considered free of pollution, and (3) from animals transferred from a nonpolluted area to areas of pollution. In addition, muscle tissue hydrolysates of specimens from the clean area were compared with hydrolysates of individuals from the polluted areas.

The sites chosen for study were a small yacht marina in the Los Angeles Harbor, designated here and in previous studies of water pollution as L.A. 7; a dock in slip I of the main channel, identified as L.A. 39; and a third area of pollution in Cerritos Channel of Long Beach Harbor, L.B. 23 (Fig. 1).

Specimens from a nonpolluted area were taken at Tomales Bay, north of San Francisco.

To establish the normal free amino acid pattern of *M. edulis*, specimens were taken from the Tomales Bay area, returned to the laboratory alive where muscle tissue was excised, quick frozen with dry ice, lyophilized, and extracted with 70% cold ethanol. Hydrolysates were prepared by hydrolysis of excised muscle with 6 N

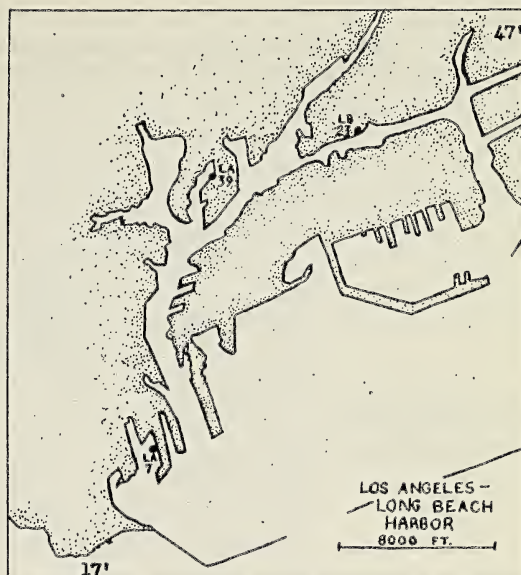


FIG. 1. Areas of pollution from which collections were made.

HCl and desalted with 70% cold ethanol. Best results were obtained by serial studies using different amounts of a given extract. By limiting the amount of extract on one paper to a minimal quantity necessary for resolution, those amino acids ordinarily present in quantities so large that adjacent spots tended to merge upon development remained distinct and compact. By placing large amounts of extract on a second paper those amino acids present in trace quantities could be detected upon development, while those present in large amounts, already determined in the first run, merged and became indistinguishable.

To determine whether or not differences in free amino acid metabolism existed in *M. edulis* under conditions of pollution, specimens were collected from polluted areas mentioned above, and treated in an identical manner.

Assuming that a difference might exist between these two groups with respect to free amino acids, as it had in other forms, an attempt was made to learn whether a change would occur following transfer from the nonpolluted to the polluted areas. Specimens from Tomales Bay were tagged for identification, placed in plastic containers through which a free exchange of water was possible, and placed in the polluted

TABLE 1

FREE AND PROTEIN-BOUND AMINO ACIDS PRESENT IN SPECIMENS OF *Mytilus edulis*
FROM THREE POLLUTED AREAS, ONE NONPOLLUTED AREA, AND TRANSFERRED SPECIMENS

	ALANINE	GLYCINE	GLUTAMIC ACID	SERINE	ASPARTIC ACID	THREONINE	LYSINE	HISTIDINE	ARGININE	VALINE/PHENYLALANINE	LEUCINES	CYSTINE	CYSTEINE	PROLINE	TYROSINE	METHIONINE	ASPARAGINE/TAURINE	UNKNOWN
Free Amino Acids Polluted areas																		
L. A. 7	×	×	×	×	×	×	×	×	×	×	×	×		×		×		2
L. A. 39	×	×	×	×	×	×	×	×	×	×	×	×		×		×		3
L. B. 23	×	×	×	×	×	×	×	×	×	×	×	×		×		×		1
Free Amino Acids Nonpolluted area																		
Tomales Bay	×	×	×	×	×	×	×	×	×	×	×			×		×		3
Free Amino Acids Transferred																		
To L. A. 39	×	×	×	×	×	×	×	×	×	×	×						×	
To L. B. 23	×	×	×	×	×	×	×	×	×	×	×						×	
Hydrolysates																		
L. A. 7	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		3
L. A. 39	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		2
L. B. 23	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		
Tomales Bay	×	×	×	×	×	×	×	×	×	×	×	×		×		×		

areas. After 10 days these specimens were removed and analyzed for free amino acid content in the manner described above. The terminal survival point for transferred animals occurred between 10 and 15 days.

RESULTS

Chromatograms made of the free amino acid extracts of specimens from clean water showed the presence of alanine, glycine, glutamic acid, serine, aspartic acid, threonine, lysine, histidine, arginine, valine, leucines, methionine, proline, plus three unidentified spots.

Native specimens from L.A. 39, L.A. 7, and L.B. 23, all polluted areas, contained alanine, glycine, glutamic acid, serine, aspartic acid, thre-

onine, lysine, histidine, arginine, valine, leucines, proline, cystine, and methionine, plus two unidentified spots in the case of L.A. 7 and three each on the chromatograms of L.A. 39 and L.B. 23. (See Table 1.)

The specimens taken from Tomales Bay and transferred to the polluted waters of L.A. 39 and L.B. 23 contained well-defined spots of alanine, glycine, glutamic acid, serine, aspartic acid, threonine, lysine, histidine, arginine, valine, leucines, and taurine/asparagine.

The hydrolysate of specimens from Tomales Bay contained alanine, glycine, glutamic acid, serine, aspartic acid, threonine, lysine, histidine, arginine, valine, methionine, leucines, cystine, and proline.

Hydrolysates of specimens from L.A. 7, L.A. 39, and L.B. 23 contained those amino acids reported above for the Tomales Bay specimens, plus tyrosine and cysteine. The spot indicative of valine assumed a shape which suggests that phenylalanine may also be present. In the case of L.A. 7 three unidentified amino acids were present also; in the case of L.B. 23, two.

DISCUSSION

An analysis of the free amino acids present in specimens from the three types of situation indicated above shows that 11 of these occurred in all forms. Those specimens taken from polluted water contained proline, cystine, and methionine as well. Those from nonpolluted water contained the proline and methionine but lacked the cystine. The chromatograms of those specimens which had been transferred from clean to polluted waters lacked all three of these free amino acids, proline, methionine, and cystine. Taurine/asparagine, not found in any of the others, either from clean or polluted water, is clearly discernible on the chromatograms of the transferred specimens.

The nature of the pollutants involved in contributing to these differences has not been specifically determined. The data compiled by the Los Angeles Bureau of Sanitation (1957), covering the periods August 1956 to February 1957, show oxygen depletion and increased coliform bacterial counts for the areas covered in this study. Reish (1960) summarizing characteristics of the areas classifies L.A. 7 and L.B. 23 as "healthy bottom" areas and lists a dissolved oxygen at 6.0 ppm for the median at the surface. He classifies L.A. 39 as "very polluted bottom" with a dissolved oxygen of 1.6 ppm. In describing the nature of the substrate he indicated the presence of black sulfide mud in each instance. A visually obvious pollutant at all three stations is an oily substance. The concentration of this at L.A. 39 is such that all submerged structures appear to have a tarlike coating. Water circulation at this point seems to be limited to that produced by tidal fluctuation.

Whatever the composition of the pollutants, they seem to contain factors which have influenced the metabolism of the sulfur-containing amino acids, cystine and methionine. It is known

that methionine can be converted to cystine, and that cystine and methionine, via cysteine, in mammals can act as a precursor of taurine. Cystine is present as a free amino acid only in those specimens from polluted water. It is protein-bound in *M. edulis* from both clean and polluted water. Methionine occurs in free form in all but the transferred specimens. It is also found as part of the proteins from *M. edulis* of both clean and polluted water. Cysteine appears only in the protein-bound form in those animals analyzed from polluted water.

If the spot that appeared in the position of taurine/asparagine on the chromatogram, is assumed to be, at least in part, taurine, then this amino acid appears in the free form in only those specimens transferred.

If the specimens taken from clean water can be considered as those with a normal metabolic pattern, then it can be safely postulated that the metabolism of methionine has not been altered in any except the transferred specimens, where it does not appear in free form. The presence of cystine as a free amino acid in individuals from polluted water suggests that some environmental factor has freed a portion of it from proteins or that an amount in excess of that utilized in protein formation has been synthesized. The possible appearance of free taurine in the transferred specimens and the total absence of free methionine suggests that some factor in the change of environment may have brought about the conversion of the latter to taurine.

The disappearance of proline in those specimens of *M. edulis* transferred from a clean to a polluted environment is unexplainable at present.

SUMMARY

In an attempt to determine the effects of water pollutants upon the wharf mussel, *Mytilus edulis*, the following analyses were made.

1. Specimens were collected from polluted waters. From these the free amino acid content of muscle tissue was analyzed by means of two-dimensional paper chromatography. These were found to contain 14 identifiable free amino acids plus some (two in one instance, three in

another) unidentifiable ninhydrin-sensitive spots.

2. Specimens from polluted waters were analyzed, after hydrolysis, for amino acid content of muscle tissue. Sixteen amino acids were identified. Unidentifiable spots also occurred in specimens from two of the three locations.

3. Specimens from nonpolluted water were treated in the same way. Thirteen free amino acids were identified. Cystine, present in free form from polluted water was lacking. Three unidentifiable spots were also present. Fourteen amino acids were identified from the protein hydrolysate. Cysteine and tyrosine, found in hydrolysates of polluted water specimens, were lacking here.

4. Specimens were transferred from clean water to polluted environments, left for 10 days, and then analyzed in the usual manner. Chromatograms showed them to have 11 free amino acids in common with the others. Proline and methionine contained in the others were absent here. Cystine, present in those native to the polluted areas, was lacking. Taurine/asparagine, not found in any of the others, appeared here.

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Important Pacific Insect Pests of Sugar Cane¹

C. E. PEMBERTON²

SUGAR CANE is commercially grown in Hawaii, Fiji, Queensland, Java, the Philippines, and Formosa. From extensive published records, some 257 insect species are known to attack cane within these several areas. The following sum-

mary will indicate only those species which have been reported as important, either occasionally or continuously, together with the nature of attack and the countries affected.

STALK BORERS

LEPIDOPTERA

Eucosmidae	<i>Eucosma schistaceana</i> Sn.	Formosa, Java, Philippines, Guam
Pyralidae	<i>Chilotraea infuscatella</i> Sn.	Formosa, Java, Philippines
	<i>Proceras venosatus</i> Wlk.	Formosa, Java, Philippines
	<i>Scirpophaga nivella</i> F.	Formosa, Java, Philippines
	<i>Emmalocera umbricostella</i> Rag.	Formosa
Agrotidae	<i>Sesamia inferens</i> Wlk.	Formosa, Java, Philippines
	<i>Sesamia uniformis</i> Dugl.	Philippines
	<i>Phragmatiphila truncata</i> Wlk.	Queensland, New Guinea

COLEOPTERA

Curculionidae	<i>Rhabdoscelus obscurus</i> Boisd.	Hawaii, Fiji, Queensland, New Guinea
	<i>Trochorrhopalus strangulatus</i> Gyll.	Philippines, Fiji, New Guinea
Prionidae	<i>Dorystenes hydropicus</i> Pascoe	Formosa

ISOPTERA

<i>Heterotermes philippinens</i> Light	Philippines
<i>Mastotermes darwiniensis</i> Frogg	Queensland
<i>Termes meridionalis</i> Frogg	Queensland
<i>Macrotermes gilvus</i> Hag.	Philippines, Java
<i>Capritermes nitobei</i> Shir.	Formosa
<i>Odontotermes formosanus</i> Shir.	Formosa
<i>Reticulitermes speratus</i> Kolbe	Formosa

DESTRUCTIVE TO SEED PIECES

COLEOPTERA

Elateridae	<i>Laeon musculus</i> Cand.	Formosa
	<i>Melanotus tamsuyensis</i> Bates	Formosa
	<i>Sephilus formosanus</i> Schwarz	Formosa
	<i>Laeon variabilis</i> Cand.	Queensland
Tenebrionidae	<i>Eutochia lateralis</i> Boh.	Java, Hawaii, Philippines

SAP SUCKERS ON LEAF OR STALK

HEMIPTERA

Lygaeidae	<i>Phenacantha australica</i> Kirk.	Queensland
	<i>Phenacantha saccharicida</i> Karsch	Java
	<i>Phenacantha marcida</i> Horv.	Formosa
	<i>Ischnodemus saccharivorus</i> Okajima	Formosa

¹ A paper presented at the Tenth Pacific Science Congress, in Honolulu, August 1962. Manuscript received February 14, 1962.

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Coccidae	<i>Aulacaspis tegalensis</i> Zhnt. <i>Aulacaspis madiunensis</i> Zhnt. <i>Saccharicoccus sacchari</i> Ckll.	Formosa, Java, Philippines Queensland, Java Queensland, Java, Formosa, Philippines, Hawaii, Fiji
Aphididae	<i>Oregma lanigera</i> Zhnt. <i>Rhopalosiphum maidis</i> Fitch <i>Aphis sacchari</i> Zhnt.	Java, Formosa, Philippines, New Guinea Hawaii, Philippines, Java, Queensland, Formosa, Fiji Hawaii, Philippines, Java, Queensland, Formosa
Aleurodidae	<i>Neomaskellia bergii</i> Sign.	Formosa, Philippines, Java, Queensland, Fiji, New Guinea
Derbidae	<i>Proutista moesta</i> Westw.	Philippines, Formosa, Java, Guam
Delphacidae	<i>Perkinsiella saccharicida</i> Kirk. <i>Perkinsiella vitiensis</i> Kirk. <i>Perkinsiella vastatrix</i> Bredd.	Queensland, Formosa, Java, Hawaii Fiji, Samoa Formosa, Java, Philippines

DESTRUCTIVE TO ROOTS AND UNDERGROUND PARTS

ORTHOPTERA		
Gryllotalpidae	<i>Gryllotalpa formosana</i> Shiraki	Formosa
COLEOPTERA		
Curculionidae	<i>Tanymecus circumdatus</i> Wied. <i>Episomoides albinus</i> Mats.	Formosa Formosa
Melolonthidae	<i>Ancylonycha borishana</i> Niiijima and Kinoshita <i>Ancylonycha vidua</i> Sharp <i>Ancylonycha helleri</i> Brenske <i>Ancylonycha leucophthalma</i> Wied. <i>Lepidiota stigma</i> Fabr. <i>Lepidiota trichosterna</i> Lea <i>Lepidiota frenchi</i> Blackb. <i>Leucopholis rorida</i> Fabr. <i>Leucopholis irrorata</i> Chevr. <i>Dermolepida albobirtum</i> Waterh. <i>Apogonia destructor</i> H. Bos <i>Rhopaea vestita</i> Arrow <i>Pseudobolophylla furfuracea</i> Burm.	Formosa Formosa Philippines, Java Java Java Java Queensland Queensland Java Philippines Queensland Queensland Java Fiji Queensland
Rutelidae	<i>Anomala limbifera</i> Ohaus <i>Anomala humeralis</i> Burm. <i>Anomala annoguttata</i> Burm. <i>Anomala orientalis</i> Waterh. <i>Euchlora pulchripes</i> Lansb. <i>Euchlora viridis</i> Fabr. <i>Anoplognathus boisduvali</i> Boisd.	Formosa Philippines Philippines Hawaii Java Java Queensland
Dynastidae	<i>Alissonotum impressicole</i> Arrow <i>Alissonotum crassum</i> Arrow <i>Alissonotum pauper</i> Burm.	Formosa Formosa Formosa, Philippines

LEAF DEFOLIATORS

ORTHOPTERA		
Acrididae	<i>Oxya chinensis</i> Thunb. <i>Locusta migratoria migratorioides</i> Rch. & Fairm. <i>Locusta migratoria manilensis</i> Meyen <i>Locusta cinerascens</i> F. <i>Locusta migratoria solitaria</i> F. <i>Hieroglyphus annulicornis</i> Shiraki <i>Gastrimargus musicus</i> F.	Hawaii Philippines, Queensland Philippines, Formosa Philippines Formosa, Queensland, Fiji, Guam Formosa Queensland
LEPIDOPTERA		
Pyalidae	<i>Hedylepta accepta</i> Butl.	Hawaii
Agrotidae	<i>Pseudaletia unipuncta</i> Haw. <i>Spodoptera exempta</i> Wlk. <i>Cirphis loreyi</i> Dup.	Philippines, Hawaii, Fiji, Queensland, Formosa, Java Philippines, Queensland, Hawaii Philippines, Java, Fiji, Queensland, Formosa

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CRAWFORD, DAVID L. 1920a. New or interesting Psyllidae of the Pacific Coast (Homop.). *Proc. Hawaii. Ent. Soc.* 4(1): 12-14.

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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

K. O. EMERY

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Studies in Fitchia

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*Device for Making Successive Photomicrographic
Records*

HAROLD ST. JOHN

*Revision of the Genus Pandanus
Part 15. Species Discovered in Thailand*

S. J. PARAMONOV

Lord Howe Island, Part III

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INSTITUTION

OCT 11 1963

An Aerial Study of Hawaiian Wave Patterns

K. O. EMERY¹

MOST OF US who have had some experience at sea on small power or sailing boats have noted that the sea surface is crossed by usually more than a single train or set of waves. Each train can be identified by its direction, period, and height. Sometimes one train is so dominant that others may not be noticed. The Marshall Islanders of the nineteenth century and earlier, past masters in the art of handling small boats, used wave trains as a navigational aid with their famous stick charts. The dominant train of waves, produced by the trade winds, was designated by long parallel sticks tied to a rigid frame. Trains of smaller waves, some produced by bending around islands, were shown by small sticks attached at angles to the long ones. A brief review of these maps and of pertinent literature was given by Emery, Tracey, and Ladd (1954:5).

A better platform than a boat for mapping waves is an airplane because of its wider field of view and greater speed. The greater speed permits observations to be made at many points in an area during a period short enough to reduce the effect of changes in winds. The first such wave maps made by aerial observation were for the sea off southern California in 1957–58 (Emery, 1958). Each of four surveys at 3-month intervals exhibited three or four trains of waves, greatly complicating the identification of waves refracted or reflected by the island or mainland shores. In order to simplify the analysis it is necessary to study an area having only a single wave train. The Hawaiian Islands were thought to constitute such an area because they lie within the belt of trade winds, especially during summer. An opportunity for study there was provided by the convening of the Tenth Pacific Science Congress at Honolulu during the latter half of August, 1961.

Through the interest of the Office of Naval Research, flight facilities were made available by Fleet Air Wing Two, Naval Air Station, Barbers Point, Oahu. The aircraft was a Neptune (P2V), having a bombardier station with excellent visibility. Acting as recorders and photographers during one flight were Charles G. Johnson (U.S. Geological Survey) and Charles Roberts (U.S. Weather Bureau); and during the other flight Robert S. Dietz (U.S. Navy Electronics Laboratory) and Joe S. Creager (University of Washington). Appreciation is also due Doak C. Cox (University of Hawaii) and Saul Price (U.S. Weather Bureau, Honolulu) for their critical reading of the manuscript.

METHODS

Flights were made on 31 August (1000–1700, local time) and 1 September (0800–1430). They covered a total distance of 4200 km at an altitude of 500 m. A total of 375 observation points were occupied at 2-min intervals. Positions of the aircraft were based upon fixes at 10–20-min intervals using loran, radar, and visual methods.

Observation was purely visual, although some photographs were taken for illustrative purposes. A specially devised pelorus was held with the aircraft's true compass heading set on the disk in a fore-and-aft direction. Moveable arms pivoted at the center of the disk were set parallel to the crests of separate wave trains, requiring constant visual checking and readjustment. At 2-min intervals the recorder noted the azimuth indicated by each arm. Comparison of results obtained at different headings of the aircraft indicate that the azimuths are correct within 10°. Estimation of the azimuth of the crests of each wave train usually required viewing in a particular direction because the waves were most clearly seen when viewed away from the sun at a horizontal angle of about 45° to the wave crests and at a downward angle of 15 to 45°. Sometimes about 10 sec of viewing was required

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Manuscript received January 10, 1962.

to identify the trains of smaller waves or waves of similar azimuths. This time requirement and the different optimum directions of viewing reduces the value of interpretation from photographs alone; in addition, photographs themselves must be interpreted later—a more difficult process than direct visual interpretation of the wave azimuths. Direct visual observation also permitted the determination of the direction of wave progress, relative to the positions of foam patches. Timing the interval between the appearance of a foam patch at the crests of successive waves provided an estimate of wave periods.

In addition to wave data, observations on wind direction and speed at the water surface were obtained. The wind direction was taken as the azimuth of the long narrow parallel wind slicks which appeared where wind speed exceeded Beaufort 3. Wind speed was estimated according to the Beaufort scale of water surface characteristics (Bowditch, 1943:52), as shown below.

BEAUFORT NUMBER	DESCRIPTION OF SEA	SPEED (KM/HR)
0	mirrorlike	0-2
1	wavelets	2-6
2	short waves	6-12
3	scattered whitecaps	12-19
4	many whitecaps	19-30
5	foam streaks	30-40

The author does not apologize for not using a more modern and sophisticated technique involving elaborate camera arrangements or electronic scanning devices, because direct observation is simpler and sufficient for the problem.

WINDS

Weather maps for the period, based upon ship and shore stations as well as upon TIROS photographs, are illustrated by Figure 1. The two high pressure areas north and northeast of Hawaii are characteristic of the season. A low pressure area about 800 km southeast of Hawaii discovered by TIROS satellite was mild and its effect was not detected during the flights. The isobars show that the wind in the vicinity of the Hawaiian Islands should have been from

about 070° (east-northeast); this is typical of the trade-wind period of the year.

A far more detailed picture of the wind pattern was provided by aerial observation (Fig. 2). On the windward side of the islands the wind speed was Beaufort 4 except adjacent to the island of Hawaii, whose blocking effect reduced the wind to below Beaufort 2. On the immediate leeward side of the islands the wind was reduced to Beaufort 1 by shielding effects. Between the islands the wind was sped by funnelling, so that a speed of Beaufort 5 occurred between Hawaii and Maui. A tongue of Beaufort 4+ extended from between Oahu and Molokai to a position off the south coast of Oahu. Verification of its presence was obtained by anemometer readings aboard R/V "Argo" of Scripps Institution of Oceanography, which worked in that area during 2 September. These tongues of high wind speed expanded and joined laterally well to the lee of Maui. However, still farther to the southwest is an area of winds less than Beaufort 3 having an unknown extent. Possibly this area is the result of the combined lees of all the islands; if so, it would be of interest to learn how much farther southwestward the area extends.

Wind direction was estimated from slicks which were long (to 500 m), narrow (a few meters), and occurred in parallel series (5-50 m apart) parallel to the wind. These wind slicks are zones of convergence between cells of surface water caused to rotate around horizontal axes by the wind (Woodcock, 1944). Oil (perhaps from phytoplankton) collects in the convergences and changes the light reflectivity and wave pattern, as observed by Dietz LaFond (1950). Other debris, including sugar mill wastes, were locally present in some slicks. The wind slicks were restricted to areas having wind speeds of Beaufort 3 or more, and are one of many phenomena which are dependent upon this critical wind speed (Munk, 1947). As shown by Figure 2 the windflow lines, deduced from the wind slicks, spread apart to pass around the islands, particularly around large and high Hawaii. Their concentration in the straits causes the high wind speeds there.

In areas having wind of less than Beaufort 3, wind slicks were usually absent. In the lee of Hawaii and Maui their place was taken by slicks

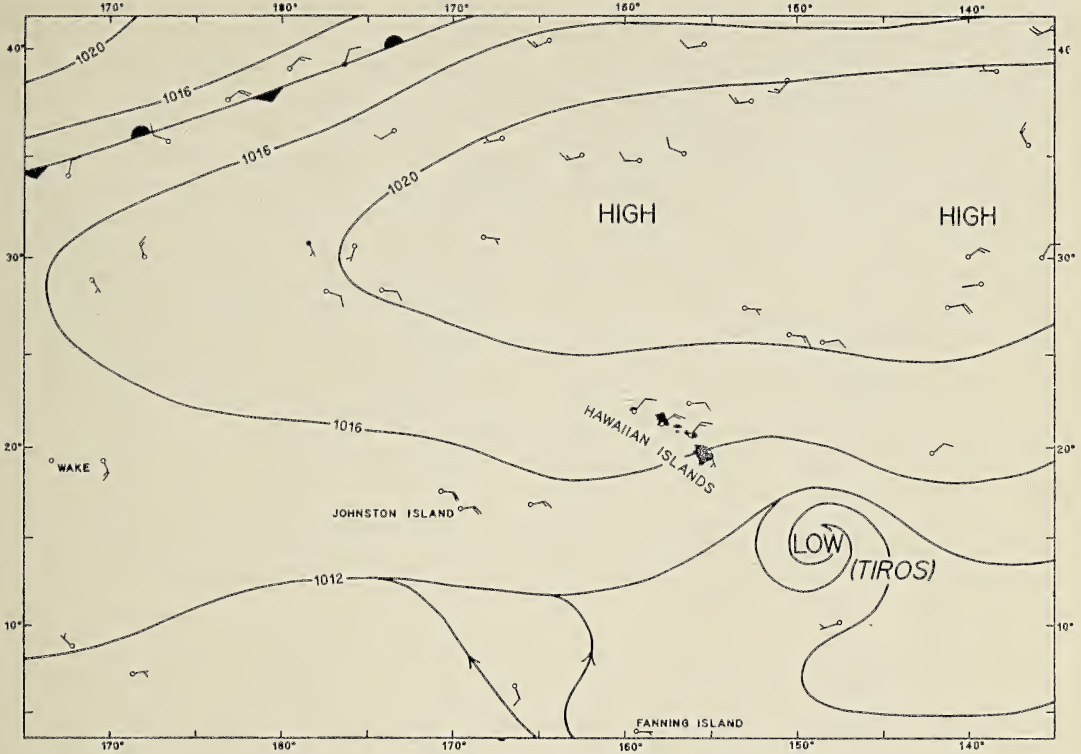


FIG. 1. Weather map for 1600 Honolulu time (0600 G.C.T.) on 31 August 1961. The winds and isobars are typical of the season for the Hawaiian Islands, except for the minor low to the southeast. Courtesy of Charles Roberts of Honolulu office of U. S. Weather Bureau.

of another kind, ones which are commonly several km long, 20–200 m wide, broadly sinuous, and 1 or more km apart. Their general trend happened to be more or less perpendicular to the wind and parallel to shore. These slicks are typical of convergences above shallow internal waves (Ewing, 1950; LaFond, 1959). A third kind of slick was noted behind a ship—straight, parallel-sided, about 30 m wide, and oily brown. It clearly resulted from ship wastes, probably from pumping of bilges or fuel tanks.

WAVES

Instead of the anticipated single train of waves, the area was found to contain three trains of large long-period waves and several trains of small short-period ones. Many measurements of the former waves revealed an average of 7-sec period, whereas the latter were 1 sec or shorter. Most of the wave energy was confined

to the two trains of 7-sec waves coming from the east (090°) and southeast (130°). The train from the east was slightly sharper crested, perpendicular to the wind slicks (compare Figs. 2 and 3), and most frequently topped by whitecaps. Interference between these two trains caused the sea surface to be broken into a diamond-shaped pattern, each block of which contained a short section of wave crest.

Along the sides of the islands, wave refraction caused the waves to bend and to approach parallelism with shore, but the width of the zone was generally too small to map on the scale of the survey. At the straits the waves took a circular front, evidently due to diffraction (Arthur, 1951). The shapes of the wave fronts are similar to those of the tsunamis studied by Shepard, Macdonald, and Cox (1950) in the Hawaiian region, but the latter are controlled more by refraction than by diffraction owing to their great wave length. Spreading of the circular

fronts beyond the straits partially filled the area leeward of the islands. Locally, complex interference patterns resulted from crossing of wave trains from different straits. In general, however, the leeward sides of the islands had only low waves of the 7-sec period. Southwest of Oahu a third train of 7-sec waves was observed moving northward; it is of unknown origin.

The waves of about 1-sec period were too short to have been produced by other than local winds. However, their round crests and large angle with the wind slicks indicate that these waves were not being formed during the time of the survey. Possibly the ones northeast of the island chain and southeast of Hawaii remained from a local wind which blew just prior to the survey; these areas were surveyed only during 31 August. The waves southwest of the chain were more irregular in pattern and may have owed their origin to cold air masses flowing down the slopes of several islands.

EFFECTS ON SHORES

During a study of beachrock in the Hawaiian Islands by Emery and Cox (1956) the shores of most of the islands were examined in detail. Others were viewed from the air during the

wave survey. These shores can be classified as follows: rocky (irregular and commonly rugged, with sea cliffs and only narrow beaches or pocket beaches), sandy (long, broad sand beaches), and muddy (mangroves, narrow beaches or none, locally with lagoons or artificial fish ponds). Ignoring transitional forms, the shore types of the islands are illustrated by Figure 4. A relationship of the shore type to the chief wave pattern, that from a generally easterly direction, can readily be observed. High storm waves from any direction (Arthur, 1948) also can control the shore types, but infrequency of the storms and inconstancy in direction of their waves reduces their importance.

Rocky shores characterize the sides of the islands most exposed to direct wave attack, except at Kaneohe Bay (east side of Oahu) where a wide offshore reef protects the shore. In some areas, such as almost the entire circumference of Hawaii, rocky shores dominate, regardless of exposure direction, probably because of the recency of volcanism. Longshore currents developed by a diagonal approach of waves to the shore have caused much of the sediment produced by wave attack of the rocky shores or of adjoining reefs to be carried beyond the areas of greatest exposure to waves. Some of

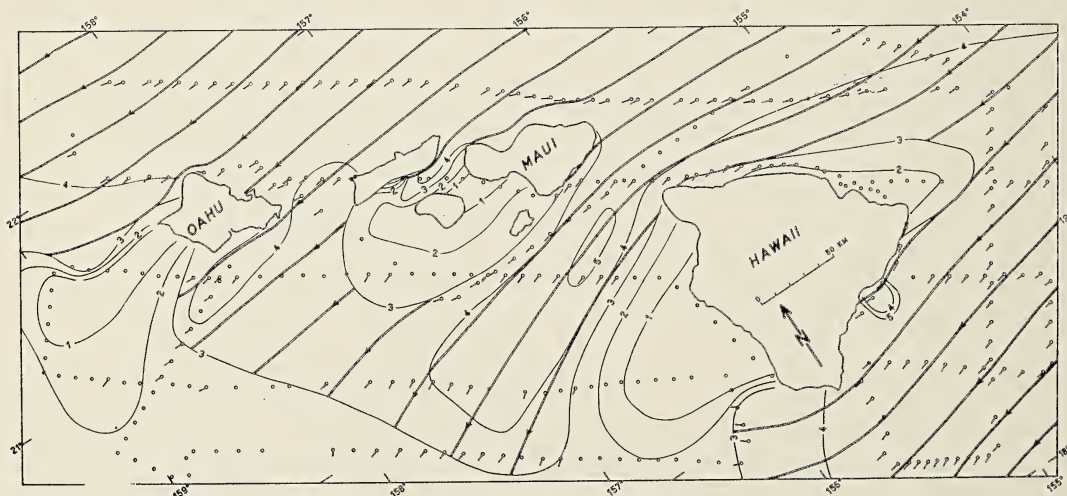


FIG. 2. Results of aerial observation of wind at sea surface on 31 August and 1 September 1961. Wind flow lines (wide lines) are based upon wind slicks observed at each position (note weather-vane line at each position). Wind speeds are based upon condition of sea surface expressed in Beaufort scale (indicated by narrow numbered lines).

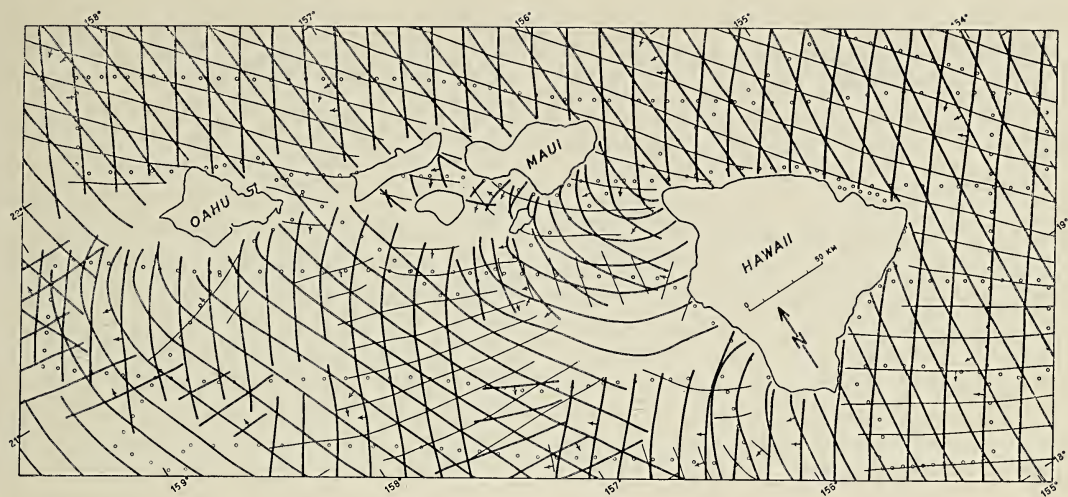


FIG. 3. Wave pattern based upon aerial observation at positions indicated by circles on 31 August and 1 September 1961. The wide lines show changing directions of crest lines of each of three different trains of 7-sec waves. The narrow lines show the same for several trains of short-period (about 1-sec) waves.

this material has been deposited to form sandy shores chiefly in the immediate lee of prominent rocky headlands where the intensity of wave attack and of longshore currents is sharply reduced. Generally this lee is west of headlands, but on Lanai it is on the east side because that side is sheltered by nearby Maui. Muddy shores are not common, but those which do exist are in areas which have the greatest protection from waves, well into the lee of the islands or of headlands.

In recent years there has been erosion of certain sand beaches, particularly those on the east side of Kauai, the north side of Oahu, and the north side of Maui. In part, this erosion has probably resulted from man's activities. However, the close relationship between shore type and degree of exposure exhibited by Figure 4 suggests another cause. As shown by Wentworth (1949), there may have been a directional change of trade winds at Honolulu from a mean of 050° in 1908 to 085° between 1925 and 1939 to 063° in 1943. If the trend is real and if it continued into recent years, the average wind direction would again have been about 050° sometime between 1950 and 1960. Although the wind direction at Honolulu may not correspond exactly with the direction of the winds at sea because of the deflecting effects of nearby mountains, the changes in wind direction

at Honolulu may well reflect changes at sea. Such a change of wind direction at sea would have produced a corresponding change of wave approach. Possibly the beaches are being shifted somewhat as weather vanes in response to this change in direction of wave approach.

SUMMARY AND CONCLUSIONS

Mapping of surface winds and wave patterns from the air is a simple procedure. A 2-day survey in the Hawaiian Islands showed that the wind was from the east, but was subject to

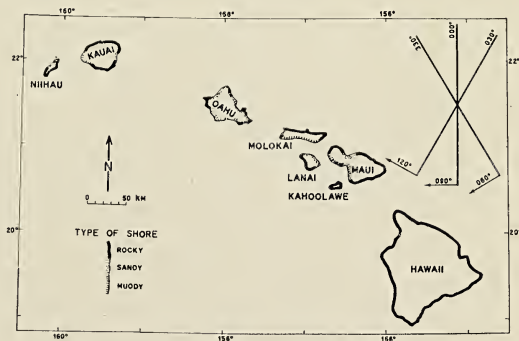


FIG. 4. Relationship of type of shore to degree of exposure to dominant waves. Radiating lines at upper right-hand corner show common azimuths of wave crests and directions of wave approach.

local deflection by the islands. It was probably typical of the trade-wind period of the year, May through September, when the winds blow from the northeasterly quadrant 80–95% of the time. From October through April the trade winds still blow from the same general direction most (65–80%) of the time (Blumenstock, 1961). The wave pattern was more complex than anticipated, with three trains of 7-sec waves and several trains of about 1-sec period. Most of the wave energy was in two trains coming from the east and southeast, evidently produced by the trade winds, and agreeing well with the general observation of predominant waves from the east in the Hawaiian region. Shore types of the islands appear to be closely related to degree of exposure to these waves. Rocky shores are generally in the most exposed sectors, sandy shores are in the immediate lee of prominent headlands, and muddy shores are in the most protected sectors. Recent changes of sandy shores may be due to possible long-term changes in the trade winds, with attendant changes in the waves produced by them.

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Solenogaster Mollusks from Southern California

MATHILDE SCHWABL¹

THE SOLENOGASTER MOLLUSKS named below were collected off southern California by the research vessel "Velero IV" of the University of Southern California, Los Angeles, California, during the course of quantitative surveys made along the shelf and slope marine bottoms from Santa Barbara, California, to south of the Mexican border. Depths of bottoms ranged from shallow shelf (about 20 m) to deep off-shore basins (about 1800 m). Most station numbers referred to in the text have been published in the Pacific Expedition series of the Hancock Foundation; they can be consulted in volumes 19 and 22. Data for additional station numbers are given in the Appendix to this report. The types of all new species and duplicates after the first are deposited in the collections of the Allan Hancock Foundation at the University of Southern California; a first set of duplicates is retained by the author.

Solenogasters have been previously recorded from California, based on collections of the USS "Albatross," and described by Heath (1911 and 1918). They were taken during dredging operations and the specimens can be only approximately located with respect to precise place, depth, and kinds of sediments.

Figures 1 and 2 plot the distributions of solenogasters taken from sea bottoms between the mainland of California and Santa Catalina Island. The dots locate the positions of intersections; they mark the even-numbered minutes of latitude and longitude, and are about 2 nautical miles apart. This area is more completely detailed in Hartman (1955). A large impoverished subsill area in the deepest part of the Channel sustains almost no life. The surrounding fringe and shelf in shallower bottoms supports characteristic kinds of solenogasters, as indicated by the symbols used in the two charts.

The diagnoses of the species require a few comments. The illustrations of the spines show only typical kinds, as these structures show strong individual variations. Nevertheless certain features, such as comparative size, being strongly keeled or not, and others, remain constant throughout the species. The small letters, *a*, *b*, *c*, *d*, used in the figures, refer to the body regions from which the spicules were taken and can be ascertained by reference to the entire figure of *Crystallophrisson recisum* n. sp.

I have come to the conviction that the so-called subradular organ of the *Crystallophrissonidae* is primarily the papilla bearing the outlets of a third group of salivary glands, which up to now has escaped the attention of other authors. It is not a sensory organ. A small number of gland follicles is situated ventrally of the fore-gut and just in front of the radula. The cells of these follicles resemble those of the lateral salivary glands, which empty their secretion through more or less well-defined ducts. An unpaired, subradular ganglion is situated among these gland follicles and was found present in each species examined; therefore, it has not been specially mentioned.

Limifossor fratula, *Crystallophrisson nanulum*, and *C. scabrum* have been described by Heath (1911, 1918); for these, abbreviated diagnoses are given.

GENUS *Limifossor* Heath, 1904

Type *L. talpoides* Heath, 1904

Limifossor fratula Heath, 1911

Heath, 1911, pp. 44, 72.

COLLECTIONS:

2189 (9) in 228 fm, with *Crystallophrisson hartmani* and *C. scabrum*.

2190 (1) in 186 fm.

2218 (1) in 249 fm, with *C. hartmani*.

2220 (3) in 180 fm, with *C. hartmani* and *C. nanulum*.

¹ Berlin Lichterfelde Kommandantenstrasse 18, Germany. Manuscript received November 22, 1961.

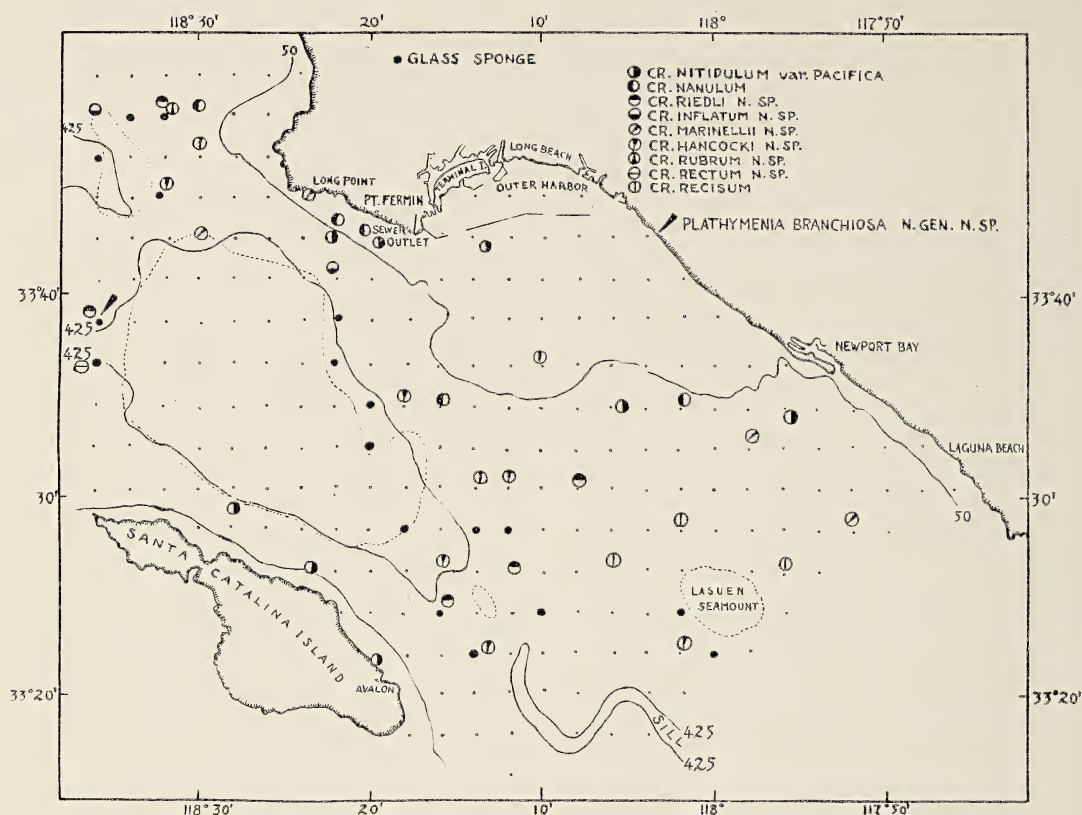


FIG. 1. The San Pedro area between the mainland of southern California and Santa Catalina Island, showing the distribution of species of solenogasters in different locations. Other data are from Hartman, 1955.

- | | |
|--|--|
| 2221 (2) in 147 fm, with <i>C. nanulum</i> . | 2500 (1) in 450 fm. |
| 2230 (1) in 300 fm, with <i>Prochaetoderma californicum</i> and <i>C. hartmani</i> . | 2612 (1) in 100 fm, with <i>C. nanulum</i> . |
| 2231 (3) in 115 fm, with <i>Crystallophrisson</i> sp. | 2625 (6) in 230 fm, with <i>C. hartmani</i> and <i>C. nanulum</i> . |
| 2293 (1) in 252 fm, with <i>C. sp.</i> | 2644 (4) in 310 fm, with <i>C. hartmani</i> and <i>C. rectum</i> . |
| 2297 (1) in 181 fm. | 2723 (2) in 325 fm, with <i>C. hartmani</i> and <i>C. hancocki</i> . |
| 2306 (3) in 215 fm, with <i>C. scabrum</i> . | 2738 (1) in 342 fm, with <i>C. hartmani</i> and <i>C. sp.</i> |
| 2329 (1) in 260 fm. | 2749 (1) in 277 fm, with <i>C. scabrum</i> . |
| 2337 (1) in 170 fm, with <i>C. sp.</i> | 2792 (1) in 300 fm, with <i>Crystallophrisson</i> sp. |
| 2361 (4) in 167 fm, with <i>C. nanulum</i> , <i>C. hartmani</i> and <i>C. sp.</i> | 2851 (1) in 230 fm, with <i>C. sp.</i> |
| 2362 (2) in 352 fm, with <i>C. hartmani</i> . | 3704 (1) in 115 fm, with <i>C. nitidulum pacifica</i> . |
| 2404 (1) in 438 fm. | 3731 (2) in 275 fm, with <i>C. incrassatum</i> . |
| 2412 (1) in 324 fm, with <i>C. hartmani</i> and <i>C. hancocki</i> . | 4756 (2) in 202.2 m. |
| 2418 (2) in 185 fm, with <i>C. scabrum</i> and <i>C. nitidulum pacifica</i> . | |
| 2430 (2) in 80 fm, with <i>C. sp.</i> | |

- 4776 (1) in 167.1 m, with *Crystallophrisson* sp.
4778 (1) in 215.8 m, with *C.* sp.
4835 (1) in 140 m.

DIAGNOSIS: The body is short, about 10 mm long; the radula is very large, distichous, and has 28 transverse rows. This organ with its muscles is heavier than that in *L. talpoides*. Dorsal salivary glands are present. The stomach and digestive glands are well developed and distinct from the intestine. Color is slate gray with a yellowish cast. Spicules from the middle of the body measure 0.5 mm long. The length index is 1.3–4.7.

DISTRIBUTION: Two individuals were reported by Heath (1911) from southern California in 260–284 fm. The present collection contains 64 specimens; 14, or 21.9%, come from depths of 77 and 150 fm; 31, or 48.8%,

are in 150 to 245 fm; 19, or 29.7%, in depths greater than 245 and 450 fm. The habitats are on various substrata, but certain kinds were selected: 52 individuals, or 81.2%, on clay, 1 on silt, 1 on rocks and mud, and 3 on clayey mud.

The station numbers refer to localities that are either in the San Pedro channel area (Fig. 2), in Santa Monica Bay to the north, or in Redondo canyon or the San Pedro Sea valley.

GENUS *Plathymenia* Schwabl, 1961

Type *P. branchiosa* Schwabl, 1961

Schwabl, 1961*b*, p. 100, figs. 1–5.

Neomeniid with short and plump body; the spicules are hollow needles. The body has a subterminal atrial opening and a terminal slit-like dorsoventral cloacal opening. Cirri in the atrial chamber are reduced; the fore-gut is

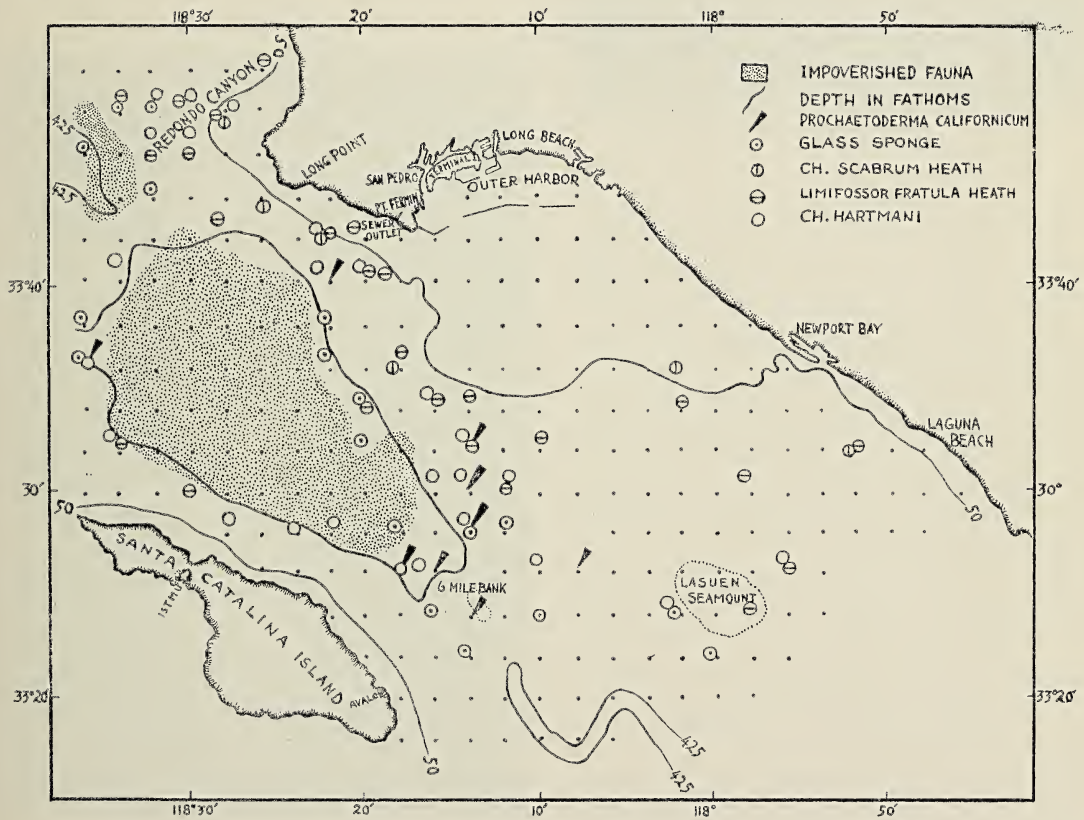


FIG. 2. The San Pedro area between the mainland of southern California and Santa Catalina Island, showing the distribution of species of solenogasters in different locations. Other data are from Hartman, 1955.



FIG. 3. *Platbymenia branchiosa*. Sta. 2324.

without a radula but has unicellular subepithelial (=dorsal diffuse) and very small ventral salivary glands; a well-developed oesophagus with villi is surrounded by numerous gland-follicles. The mid-gut is largely divided into diverticles, and the gonads also have large lateral diverticles. The brain is bilobed, has a dorsoterminal organ of the *Entonomenia* type. The shell-gland has subepithelial glands; there are no copulatory organs.

The genus is known for a single species, *P. branchiosa* Schwabl.

Platbymenia branchiosa Schwabl, 1961

Fig. 3

Schwabl, 1961*b*, p. 100, figs. 1-5.

COLLECTION: 2324 (1) in 400 fm, with *Crystallophrisson riedli* n. sp.

DIAGNOSIS (translated from the German): The species has the characteristics of the genus. The body is flattened ventrally; length of the body is 10 mm, width 2.5 mm. There is no

dorsal keel but a tapering front end and a broadened or rounded hind end. Color in alcohol is muddy gray. The cuticle is heavy and there are no epidermal papillae. The spicules are hollow, straight or slightly curved needles, the radial ones up to 700 μ long, the tangential ones up to 100 μ . The ventral furrow is distinctly separated from the cloacal opening, one single ventral fold. About 30 sensory setae in epidermal pockets surround the atrial opening. The muscles are very weak. The parenchyma of the hind end has a gelatinous basic substance. The pericardium is very large and has short distal appendages. The ventricle for half its length is dorsally connected with the pericardium, the auricle is free, and has two atrio-ventricular openings. A large cloacal chamber has about 110 simple radial gill-folds. There are no abdominal spicules.

DISTRIBUTION: This species is known through a single specimen from the San Pedro area, in 400 fm, in mud with glass sponge.

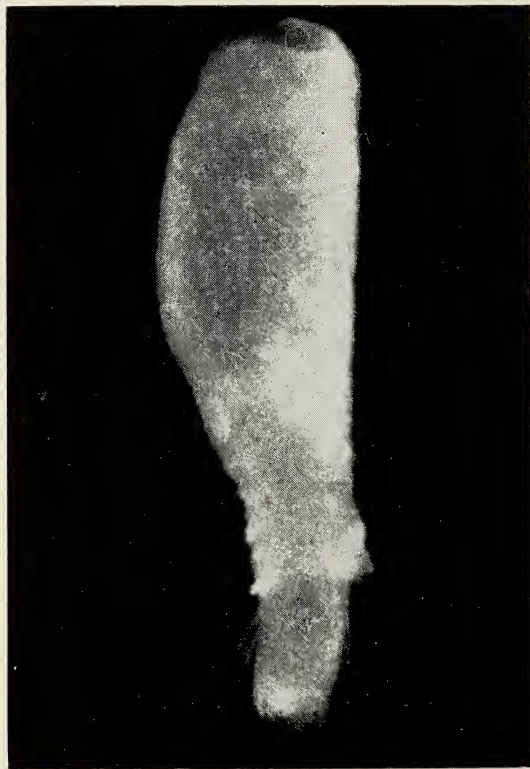


FIG. 4. *Prochaetoderma californicum* n. sp. Sta. 2802-54.

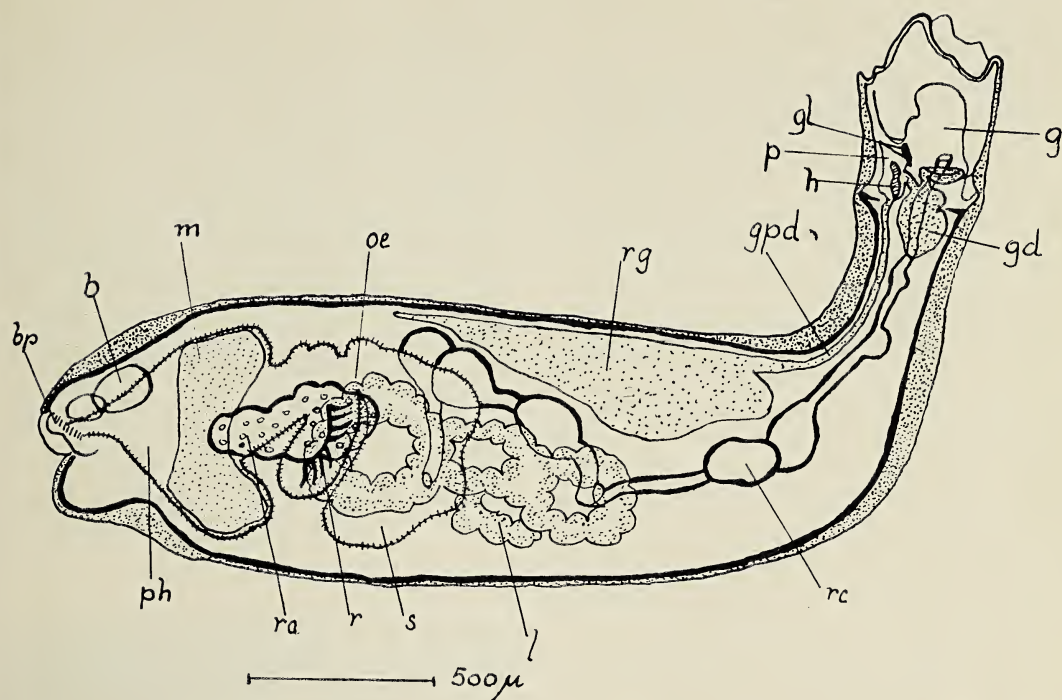


FIG. 5. *Prochaetoderma californicum*. Diagram of entire animal, showing arrangement of internal organs. *b*, Brain; *bp*, buccal plate; *g*, gill; *gd*, gonoduct; *gpd*, gonopericardial duct; *gl*, ganglion; *h*, heart; *l*, liver; *m*, mandible; *oe*, oesophagus; *p*, pericardium; *ph*, pharynx; *r*, radula; *ra*, radula cartilage; *rc*, rectum; *rg*, reproductive gland; *s*, stomach.

GENUS *Prochaetoderma* Thiele, 1902

Type *P. raduliferum* (Kowalevsky) 1901

2899 (3) in 335 fm.

3037 (1) in 360 fm.

Prochaetoderma californicum n. sp.

Figs. 4–7

COLLECTIONS:

2228 (1) in 293 fm.

2230 (3) in 300 fm, with *Limifossor fratula* and *Crystallophrisson hartmani*.

2321 (34) in 385 fm, with *C. hartmani* and *C. sp.*

2363 (2) in 429 fm, with *C. marinellii* and *C. sp.*, juv.

2411 (4) in 400 fm, with *C. hartmani*, *C. hancocki*, and fragments.

2798 (5) in 386 fm, with *C. hartmani* and *C. recisum*.

2802 (1) in 420 fm, with *C. hartmani*.

2837 (2) in 454 fm, with *C. hartmani*.

2839 (6) in 446 fm, with *C. hartmani* and *C. hancocki*.

DIAGNOSIS: These very small animals measure 2.25 to 3.05 mm in length; greatest diameter is 0.42–0.85 mm; they show a very characteristic habitus (Fig. 4); a short head region is not separated from the following trunk region (Fig. 5) but is distinguished from it by the spines, which are small leaflike structures (Fig. 7), densely arranged and mostly standing upright on the body wall. The following region, occupying the greater part of the body and containing such main organs as stomach or mid-gut, liver, and gonads, is covered by flat imbricating spines arranged obliquely towards the dorsal midline of the body. The tail-like hind part of the body is provided with spicules resembling those of the head region but of larger size. The terminal end, containing part of the gonoducts, pericardium, and cloacal chamber with its organs, is protected by a

brushlike wreath of long and pointed thorn-like spicules.

The mouth opening is flanked by the paired triangular buccal plate, and the entire front end can be withdrawn into the semicircular groove. The subepidermal muscle layers, with the exception of those in the tail region, are very weak, and the diagonal one is almost totally lacking. Three pairs of distinct retractors in the front end, and six pairs of gill retractors, pass laterally from the pericardium and are present with the thick radula muscles.

The nervous system consists of paired brain lobes, the two halves connected by a strong commissure and of three pairs of precerebral ganglia. The buccal connective leaves the brain separately, whereas the lateral and ventral ones have a common root. The buccal system consists of three ventral commissures and a single dorsal one; an unpaired subradular ganglion is present.

The digestive tract begins with a wide phar-

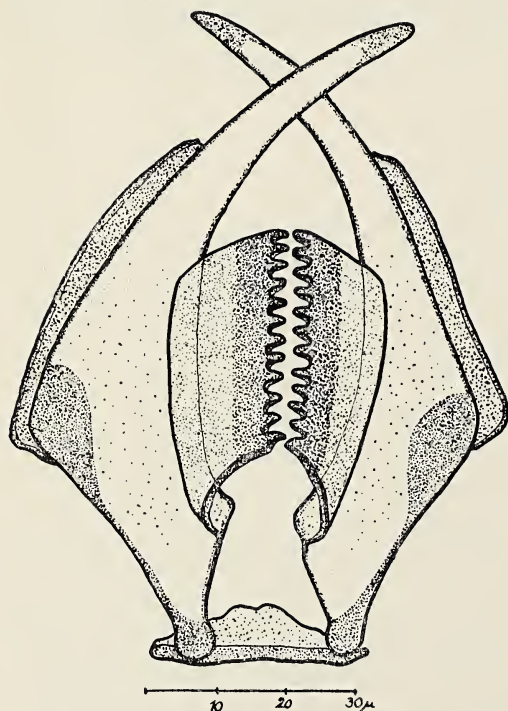


FIG. 6. *Prochaetoderma californicum*. A transverse row of the distichous radula, showing basal plate, tooth, and lateral plate.

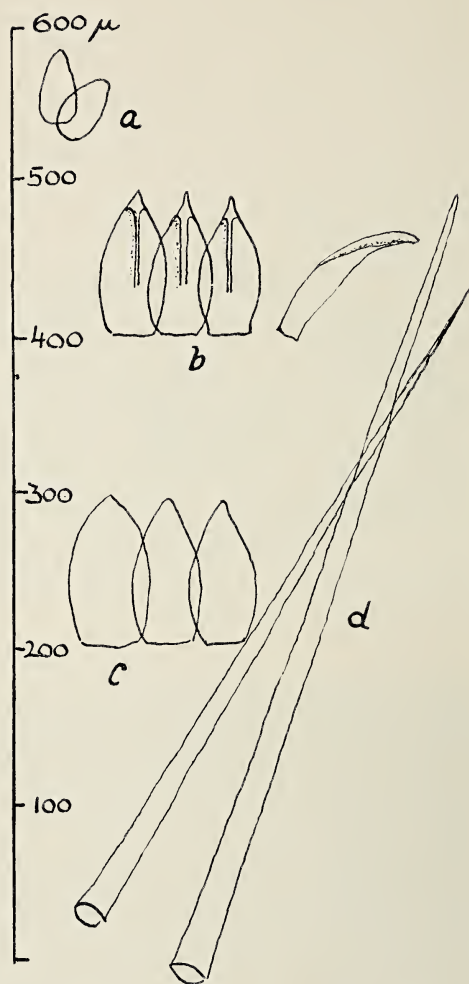


FIG. 7. *Prochaetoderma californicum*. Different kinds of spines from body regions *a*, *b*, *c*, *d*, illustrated in Fig. 9.

ynx, its epithelium bearing a distinct cuticle which, in two large lateral pockets, is differentiated into a pair of mandibles. Small salivary glands are developed at the junction of the pharynx and the short ciliated oesophagus. A glandular subradular organ lies in front of the large distichous radula; it consists of 9–12 transverse rows of teeth (Fig. 6) and is situated in a distinct radular sack. The oesophagus connects with a short wide stomach from which the long rectum and the short sacculate liver originate.

The reproductive organs consist of a short reproductive gland, a long unpaired (!) gonopericardial duct, and the typical gonoducts with their ciliated glandular parts. The pericardium is wide and short, its appendages unite ventrally and surround the supra-rectal ganglion as well as the distinct gill-sinus, but do not extend backwards along the cloacal chamber. Blood cells are present. The animal possesses two pairs of gills of a rather primitive structure.

DISTRIBUTION: Southern California, chiefly in the San Pedro area; 62 specimens all from considerable depth, between 293 and 454 fm. Eleven samples were taken, 9 from mud (5 in the glass sponge area), and only 2 samples (with 4 specimens) came from other than mud (gravel or sandy mud). Figure 4 shows one from station 2802.

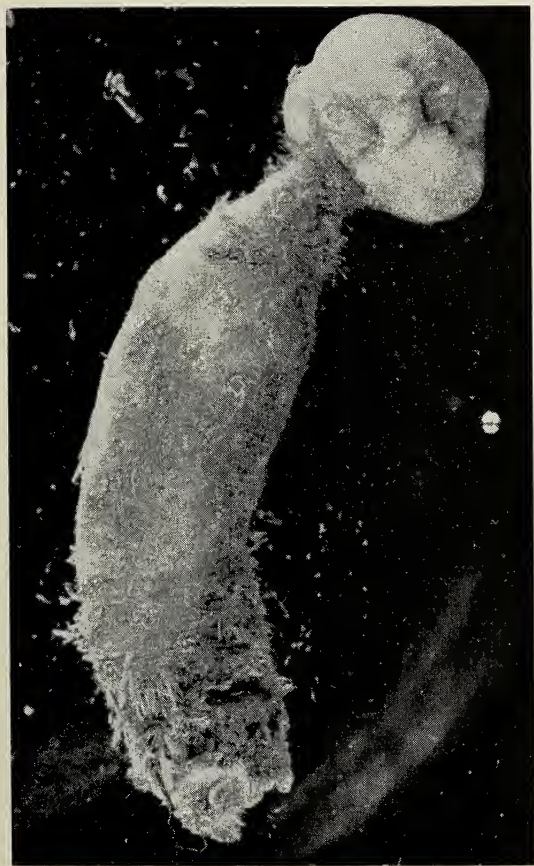


FIG. 8. *Crystallophrisson incrassatum*. Sta. 3831-55.

GENUS *Crystallophrisson* Möbius, 1875

Type *C. nitidulum* (Lovén) 1844

Includes *Chaetoderma* Lovén, 1845, preoccupied in Pisces by Swainson, 1839 (see Thiele, 1932).

Crystallophrisson incrassatum n. sp.

Fig. 8

COLLECTIONS:

3731 (2) in 275 fm, with *Limifossor fratula*.

3733 (2) in 305 fm.

DIAGNOSIS: The animals were very poorly preserved; the diagnosis therefore is largely based on external appearances.

Spicules were totally lacking but the species obviously possessed these structures originally. The habitus is very characteristic (Fig. 8). The body is very stout; the length ranges from 12-17 mm, the greatest diameter between 3 and 4.5 mm, and the length index is 4-5. The prothorax is white, highly swollen, and may attain a third of the total length of the animal. Color of the body is gray, covered with mud. The metathorax is slender and short; the preabdomen is swollen and contains the particularly large liver. The postabdomen forms a characteristic conical ring around the cloacal opening; the gills are mostly protruding from the cloacal chamber. Buccal, dorsal, and lateral salivary glands are present. A "tongue" is provided with a sharp chitinous edge on both sides behind the main tooth, but real teeth are lacking. There are four pairs of precerebral ganglia. The muscles consist of one pair of dorsal and some pairs of lateral retractors at the front end. Granular cells are also situated on the numerous septa dividing the liver into countless lobules.

DISTRIBUTION: This is known only from the Santa Barbara basin, southern California, in about 300 fm, in mud. Fig. 8 an individual in station 3731.

Crystallophrisson recisum n. sp.

Figs. 9, 10

COLLECTION: 2895 (1) in 265 fm.

DIAGNOSIS: This is a small species, measuring 11 mm long, with an average diameter of

2 mm. Color of the body is light brown. The rather swollen prothorax (Fig. 9) measures about a third of the entire length. The rounded buccal plate is pierced by the mouth opening. The spicules (Fig. 10), including the small ones, are distinguished by a distinct keel; the pointed thornlike spicules of the hind end bear conspicuous brown incrustations. With the exception of the gill retractors, the muscles are fairly weak; the longitudinal ones split up into five or six bundles on each side before giving origin to two pairs of dorsal and three pairs of lateral retractors of the front end. Among the usual six pairs of gill retractors, the dorsal posterior ones are markedly thick and partly attached to the wall of the cloacal chamber between the two gills. The posterior vertical

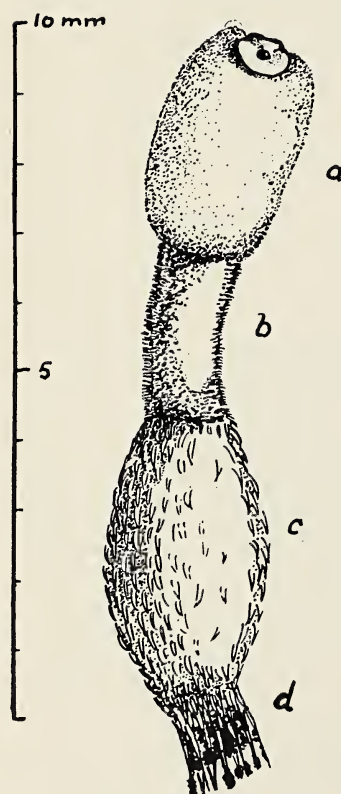


FIG. 9. *Crystallophrisson recisum*. Entire animal in side view, showing the body regions, *a*, *b*, *c*, *d*, from which are taken the spines named in the text.

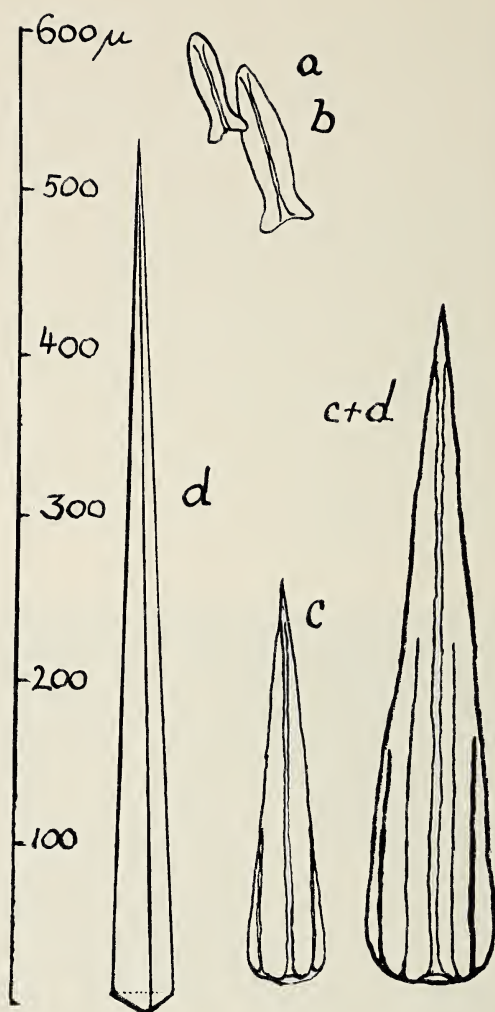


FIG. 10. *Crystallophrisson recisum*. Spines from body regions, showing characteristic ones from regions *a*, *b*, *c*, and *d*. (Compare with Fig. 9.)

diaphragm is very strong. Three free gill-lamellae on each side arise from the cloacal wall. The nervous system is typical; the location of the brain is rather far back above the radula. The cerebro-buccal connective is split off the common trunk shortly behind its origin. The narrow fore-gut possesses a very strong sphincter some distance from the mouth opening; buccal glands are to be found only in front of it. The three kinds of salivary glands are present but are unusually small; the radula is

provided with two small denticles; the cuticle of the tongue is thin but highly chitinous. The cuticular ridge on the dorsal wall of the midgut is near the opening of the liver, and a rectum is present. Granular cells occur on the dorsal wall of the liver and on the edges of the septa which divide the liver into numerous lobules. The pericardium is spacious; the heart is typical and has two atrioventricular openings. The gonoducts open on papillae; their epithelium is not continued on the wall of the cloacal chamber.

DISTRIBUTION: This has been found only once, in the San Pedro area of southern California, in 265 fm, on gray green mud.

Crystallophrisson scabrum Heath, 1911

Heath, 1911, pp. 44, 63, pl. 4, figs. 2, 16, pl. 29, figs. 6, 7, 9-11, pl. 30, figs. 1, 3, pl. 37, fig. 19.

COLLECTIONS:

- 2189 (12) in 228 fm, with *Limifossor fratula* and *C. hartmani*.
 2306 (1) in 215 fm, with *Limifossor fratula*.
 2357 (1) in 100 fm.
 2418 (13) in 185 fm, with *Limifossor fratula* and *C. nitidulum pacifica*.
 2749 (1) in 277 fm, with *Limifossor fratula*.
 2793 (2) in 251 fm, with *C. sp.*

DIAGNOSIS: This is a rather small species, 10-12 mm in length, and 2 mm in greatest diameter. The region of the liver is greenish, and the hind end has brown incrustations. The prothorax is short and swollen, and the second half of the body is considerably thickened. The mouth opening is rather large and surrounded by the round buccal plate. Compact groups of gland cells occur mainly on the dorsal side of the fore-gut. The pericardium is large and the heart highly muscular. The cloacal chamber is small.

DISTRIBUTION: This species was originally described from Monterey Bay in 715 fm (Heath, 1911); the present records are from the San Pedro area, including Redondo canyon, in depths of 100-277 fm, in mud.

Crystallophrisson hartmani Schwabl, 1961

Figs. 11, 12

Schwabl, 1961a, pp. 258-277, figs. 1-10.

COLLECTIONS:

- 2150 (3) in 310 fm, with *C. rubrum* and *C. riedli*.
 2189 (1) in 228 fm, with *C. scabrum* and *Limifossor fratula*.
 2218 (1) in 249 fm, with *Limifossor fratula*.
 2220 (1) in 180 fm, with *Limifossor fratula* and *C. nanulum*.
 2223 (1) in 480 fm, with *C. sp.*
 2230 (2) in 300 fm, with *Limifossor fratula* and *Prochaetoderma californicum*.
 2299 (1) in 360 fm.
 2301 (1) in 335 fm.
 2302 (1) in 185 fm, with *C. sp.* (used for Fig. 12, left).
 2321 (1) in 385 fm, with *Prochaetoderma californicum* and *C. sp.*
 2361 (1) in 167 fm, with *Limifossor fratula*, *C. nanulum* and *C. sp.*

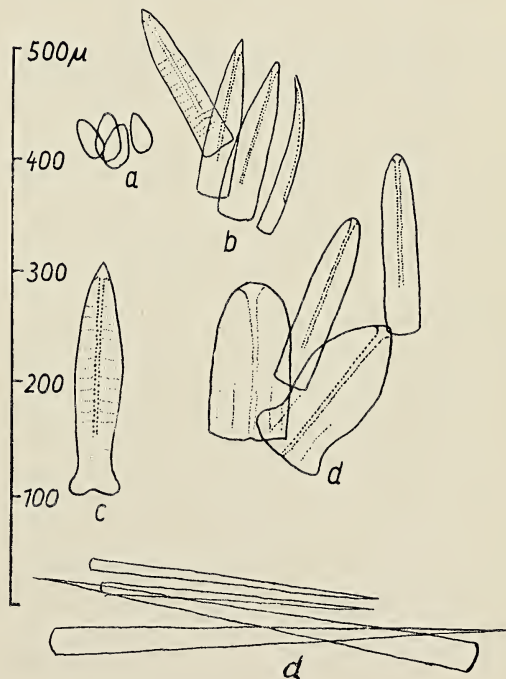


FIG. 11. *Crystallophrisson hartmani*. Characteristic spicules from body regions a, b, c, d.

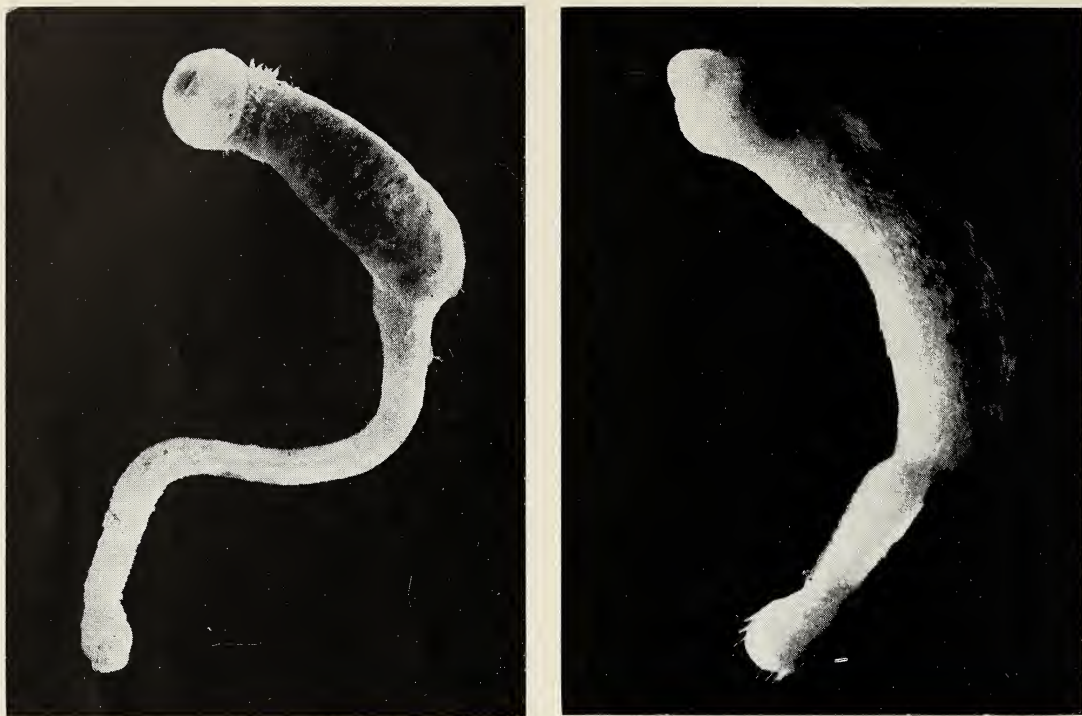


FIG. 12. *Crystallophrisson bartmani*. Left, Sta. 2302-53. Right, Sta. 2644-54.

- 2362 (1) in 352 fm, with *Limifossor fratula*.
 2410 (1) in 410 fm, with *C. hancocki*.
 2411 (2) in 400 fm, with *Prochaetoderma californicum* and *C. hancocki*.
 2412 (1) in 324 fm, with *Limifossor fratula* and *C. hancocki*.
 2441 (3) in 340 fm.
 2625 (2) in 230 fm, with *Limifossor fratula* and *C. nanulum*.
 2642 (4) in 422 fm.
 2644 (2) in 310 fm, with *Limifossor fratula* and *C. rectum* (see Fig. 12, right).
 2723 (1) in 325 fm, with *Limifossor fratula* and *C. hancocki*.
 2738 (2) in 342 fm, with *Limifossor fratula* and *C. sp.*
 2795 (1) in 290 fm, with *C. sp.*
 2798 (3) in 386 fm, with *Prochaetoderma californicum* and *C. rectum*.
 2802 (2) in 420 fm.
 2837 (2) in 454 fm, with *Prochaetoderma californicum* and *C. sp.*
 2839 (4) in 446 fm, with *Prochaetoderma californicum* and *C. hancocki*.

- 2846 (2) in 612 fm.
 3019 (4) in 425 fm, with *C. sp.*

DIAGNOSIS: Length of body 5-18 mm, width of body in front 0.8-2 mm, posteriorly 0.4-0.6 mm. The anterior half of the body, containing the short liver, is swollen; the posterior half is slender and tail-like, terminating in a button-like posterior end (Fig. 12). The head region is whitish and the rest of the body is yellowish-brown with dark incrustations on the hind end. The buccal plate is round, and the terminal opening of the cloacal chamber is surrounded by longer and shorter thorns. The spicules (Fig. 11) of the anterior end are small and squamiform; those of the rest of the body are lancet-like or leaflike and have a keel. The four groups of longitudinal muscles are limited to the posterior half of the body; one pair of dorsal and one of lateral retractors occur anteriorly. There are five pairs of gill retractors. The nervous system consists of four pairs of precerebral ganglia. One pair of small ganglia connects with the buccal ganglia near the junc-

tion of fore- and mid-gut. Buccal glands and lateral and dorsal salivary glands are present. The radula has one pair of sickle-like teeth, one pair of small lateral teeth, and an unpaired piece. The mid-gut bears a cuticular stripe dorsally. The liver has granular cells which are present also at the end of the irregular septa. Gill lamellae number 15–20. The heart is muscular and has two atrioventricular openings.

DISTRIBUTION: This species occurs commonly in the San Pedro area of southern California, in depths of 330–1100 m, in sediments of mud or clay. It is frequently found in glass sponge associations.

Crystallophrisson nanulum (Heath) 1911

Fig. 13

Chaetoderma nanula Heath, 1911, pp. 66–67, pl. 4, figs. 1, 12, pl. 27, fig. 3, pl. 28, figs. 7, 10, 11, 12, pl. 37, fig. 18.

COLLECTIONS:

2220 (7) in 180 fm, with *C. hartmani* and *Limifossor fratula*.

2221 (2) in 147 fm, with *Limifossor fratula*.

2361 (2) in 167 fm, with *Limifossor fratula*, *C. hartmani* and *C. sp.*



FIG. 13. *Crystallophrisson nanulum*. Sta. 2220.

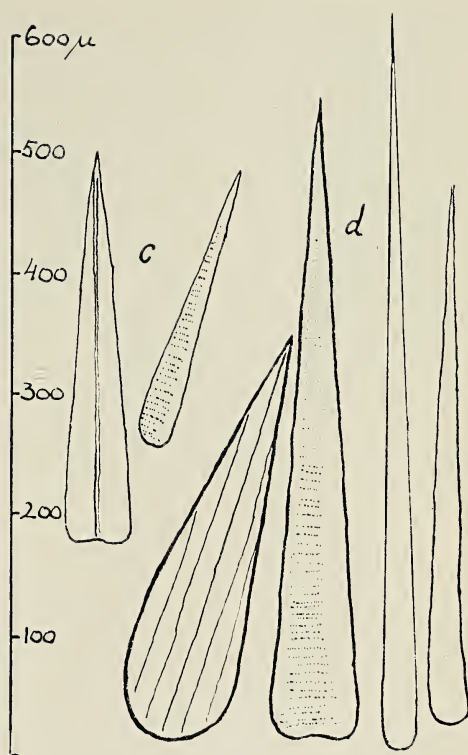


FIG. 14. *Crystallophrisson bancocki*. Characteristic spicules from body regions *c* and *d*.

2612 (1) in 100 fm, with *Limifossor fratula* and *C. sp.*

2625 (1) in 230 fm, with *Limifossor fratula* and *C. hartmani*.

DIAGNOSIS: The body is small, comparatively stout (Fig. 13), and measures 7–9 mm long and up to 1.2 mm at its greatest width. The spines are keeled and appear heavy. The color of the body is yellowish-brown. The radula is small and has two small denticles. Salivary glands are reduced to a small group of cells near the radula.

DISTRIBUTION: This was originally described based on a single specimen from southern California, in 260–284 fm. The present collections include 13 specimens, all from the San Pedro area, in depths of 100–230 fm, and always associated with *Limifossor fratula* in sediments of green or sandy mud.

Crystallophrisson hancocki n. sp.

Figs. 14, 15

COLLECTIONS:

- 2411 (2) in 400 fm, with *Prochaetoderma californicum* and *C. hartmani*.
 2412 (1) in 324 fm, with *Limifossor fratula* and *C. hartmani*.
 2475 (1) in 405 fm.
 2497 (1) in 24 fm.
 2628 (1) in 350 fm.
 2641 (1) in 373 fm.
 2723 (2) in 325 fm, with *Limifossor fratula* and *C. hartmani*.
 2839 (2) in 446 fm, with *C. hartmani* and *Prochaetoderma californicum*.
 2888 (1) in 390 fm.
 2901 (2) in 310 fm.

DIAGNOSIS: This species is of moderate size and measures between 19 and 25 mm long, with a fairly large prothorax (Fig. 15). The color in alcohol is brownish-gray. The spines are large but weak, and most of them lack a marked keel (Fig. 14). The body is distinctly narrowed between the preabdomen and the slender and somewhat elongated postabdomen; on the latter the slitlike dorsoterminal sense organ is clearly visible. The buccal plate is rounded and pierced by the mouth opening

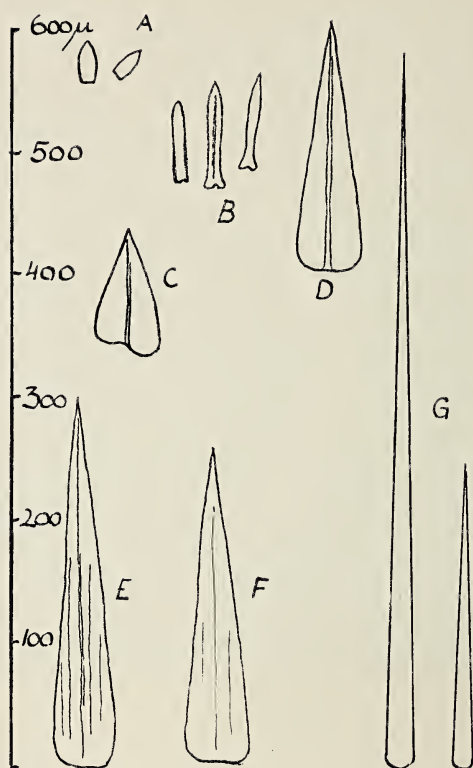
FIG. 15. *Crystallophrisson hancocki*. Sta. 2839.

FIG. 16. *Crystallophrisson nitidulum* var. *pacifica*. Characteristic spicules from body regions *a*, *b*, *c*, *d*, and other spines, labeled *E*, *F*, *G*, discussed in the text.

near its dorsal edge. A glandular zone on the postabdomen and moderate incrustations of the latter are present. The subepidermal muscle layers are fairly strong, even in the region of the liver; in the prothorax the longitudinal layer splits up at once into numerous bundles. One finds several pairs of ventral, dorsal, and lateral retractors; the gill-retractor muscles are typical. The nervous system is characterized by a brain more clearly bilobed than usual, by a cerebrobuccal nerve split off the one common trunk shortly behind its origin, and by a supra-rectal ganglion surrounded by the pericardium.

The digestive tract begins with a narrow fore-gut; its sphincter muscle is very strong. Buccal glands are observed only in front of it. Small ventral salivary glands with outlets on a very marked papilla; small dorsal ones behind

the radula and particularly large lateral ones extend from the radula to the junction of the fore-gut with the mid-gut. The radula is large and highly chitinous but without denticles. It extends far into the lumen of the fore-gut and has unusually large supports. The mid-gut and rectum are spacious. The pericardium is not very wide but extends far proximally. The ventricle is muscular and has two atrioventricular openings. The dorsal vessel begins with a bulb. The epithelium of the gonoducts continues for some distance on the wall of the cloacal chamber.

DISTRIBUTION: All specimens come from the San Pedro area, southern California, and all but one from depths between 310 and 446 fm. Eleven, or 78.5%, are from mud, and 5, or 35.7%, from glass sponge areas.

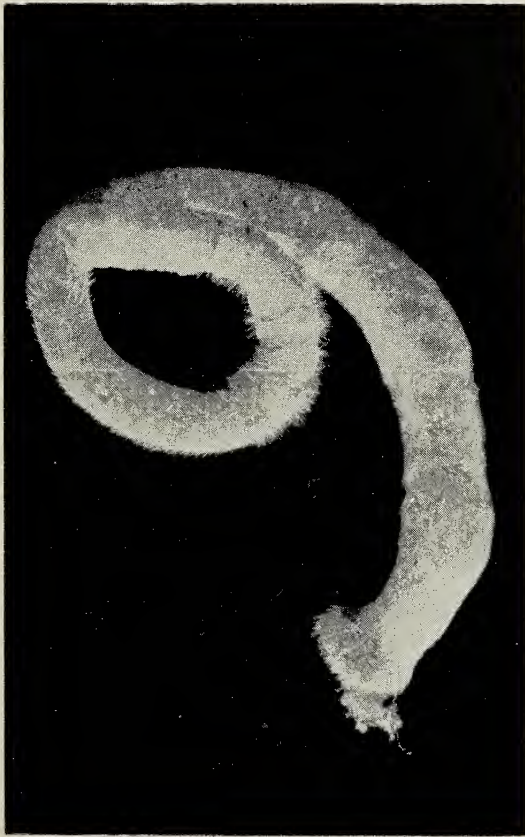


FIG. 17. *Crystallophrisson nitidulum* var. *pacifica*. Sta. 2176.

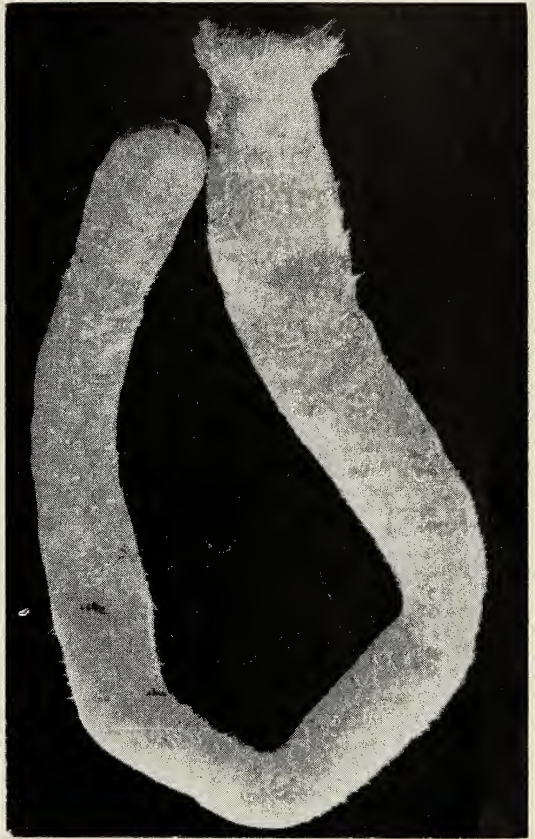


FIG. 18. *Crystallophrisson nitidulum* var. *pacifica*. Sta. 2418.

Crystallophrisson nitidulum (Lovén) 1844,
stem species

Crystallophrisson nitidulum var. *pacifica* n.
var.

Figs. 16–18

COLLECTIONS:

- 2121 (1) in 32 fm, with *C. sp.*
- 2168 (1) in 12 fm.
- 2176 (3) in 28 fm.
- 2417 (1) in 34 fm, with *C. sp.*
- 2418 (2) in 185 fm, with *Limifossor fratula*
and *C. scabrum*.
- 2614 (2) in 155 fm.
- 2457 (1) in 111 fm.
- 2743 (1) in 150 fm.
- 3204 (1) in 115 fm, with *Limifossor fratula*.
- 3205 (1) in 88 fm, with *C. sp.*

DIAGNOSIS: Overall length is 20–40 mm; greatest width 1.0–2.5 mm, the largest specimens coming from greater depths. This variety of the well-known *C. nitidulum* Lovén agrees with the stem species in its outer appearance. Characteristic are the not very swollen prothorax, the outline of the buccal plate, the short but clearly visible dorsoterminal sense organ, and its inner organization showing the development and number of muscles of the stem. The nervous system is like that of its stem species, and the radula similarly has two denticles. Other similarities include the structure of the liver, the epithelium of the gonoducts

and anus which continues for a great distance on the cloacal wall, and above all by the presence of only one atrioventricular opening.

The variety differs from the stem species by its greyish color and by the short but widely expanded postabdomen (Figs. 17, 18), which contains a large blood sinus surrounding the cloacal chamber, reducing the latter to an unusually small cavity. The spines (Fig. 16) corresponding to those of type C (see Fig. 9), which are characteristic of the stem form, occur only sparsely, whereas spines of types B, E, and G (the last only on the postabdomen) are abundant. On smaller specimens the spicula of type F could be found in great numbers on the metathorax, pre- and postabdomen; on larger specimens they were replaced by spines of type D, showing a distinct keel. Characteristic of the variety is the large, clearly outlined atrium of the heart which surrounds the supra-rectal ganglion.

DISTRIBUTION: The stem species has been widely recorded from both sides of the north Atlantic Ocean, the west coast of Sweden, Norway, Iceland, the North Sea, the eastern coast of North America from New Foundland to Virginia, and the West Indies; depths have ranged from 20–2250 m. The new variety is known through 14 specimens coming from the San Pedro area of southern California, in depths of 12–185 fm, in sediments of mud, sandy mud (2 specimens), and sandy clay (1 specimen).

Crystallophrisson riedli n. sp.

Figs. 19, 20

COLLECTIONS:

- 2150 (2) in 310 fm, with *C. bartmani* and *C. rubrum*.
 2324 (1) in 400 fm, with *Plathymenia branchiosa*.
 2352 (1) in 420 fm.
 2414 (1) in 177 fm.
 2838 (1) in 394 fm.

DIAGNOSIS: Individuals range in length from 15–22 mm and have an average diameter in the prothorax of 2 mm. Alcohol preserved specimens are gray with a whitish prothorax. In fixed state the posterior half of the prothorax

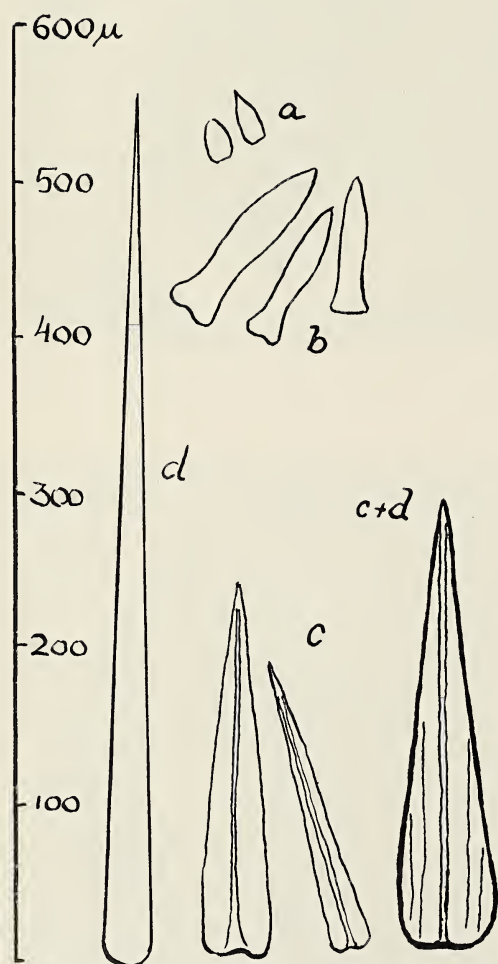


FIG. 19. *Crystallophrisson riedli*. Characteristic spines from body regions a, b, c, and d.



FIG. 20. *Crystallophrisson riedli*. Sta. 2838.

is frequently more contracted than the anterior half (Fig. 20). The dorsoterminal organ is very short but continuous with the opening of the cloacal chamber. The buccal plate is rounded and has a dorsal cleft containing the mouth opening. The abdominal gland zone is present. Spines (Fig. 19) are of medium size and have a marked keel.

Dorsal, lateral, and ventral retractor muscles are present at the front end; the longitudinal muscle layer in the prothorax is gradually split up into numerous bundles. The gill retractors are short; the ventral anterior ones are very heavy; the second pair of dorsal posterior ones are lacking or, if present, attach to the cloacal wall between the gills. Lateral, ventral, and part of the dorsal anterior gill retractor unite before entering the gill, which gives the transverse section of the gill a very characteristic appearance. The gill axis consists of a bulbous

ventral half, and a very slender dorsal half. The posterior vertical diaphragm is unusually strong.

The nervous system is typical; the buccal nerve leaves the common root very soon. The fore-gut has a strong circular and longitudinal muscle layer, circular in outline. Numerous buccal glands occur behind the sphincter muscle. All three kinds of salivary glands are present but the ventral ones are very small. The radula is typical. Granular cells in the liver are not only concentrated on the dorsal wall but irregularly distributed. The circulatory organs are typical, with two atrioventricular openings. The gonopericardial duct is fairly long and curved; the ciliated part of the gonoducts is comparatively long. The openings of the gonoducts are mostly on flat papillae, and their epithelium is not continued on the wall of the cloacal chamber.

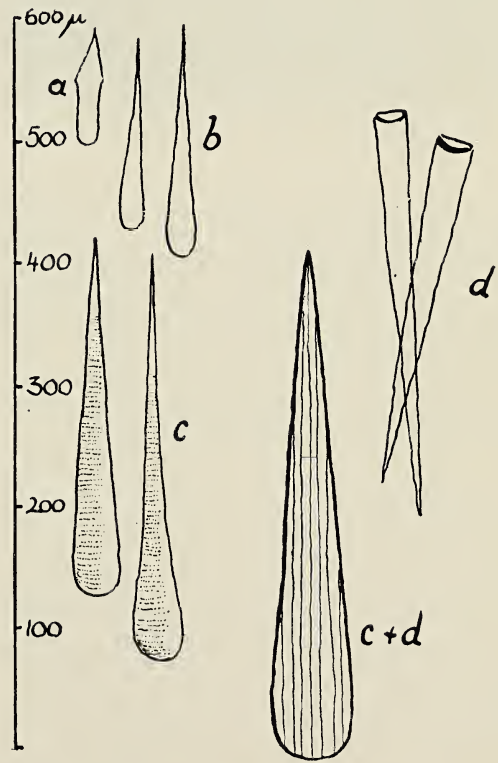


FIG. 21. *Crystallophrisson inflatum*. Characteristic spicules from body regions *a*, *b*, *c*, and *d*.



FIG. 22. *Crystallophrisson inflatum*. Sta. 2791.

DISTRIBUTION: This species is known through six specimens, all from the San Pedro area including Redondo canyon, southern California, in depths of 177–420 fm. Three were found in mud, one in mud and gravel, and one in coarse sand.

Crystallophrisson inflatum n. sp.

Figs. 21, 22

COLLECTIONS:

2110 (3) in 427 fm.

2791 (2) in 415 fm.

DIAGNOSIS: This is a large species, with total length ranging between 25 and 35 mm, and greatest width 4 mm; the prothorax region is greatly inflated (Fig. 22). The hind end is provided with two lateral prolongations of the body wall which can be withdrawn into the cirlet of thorns protecting the opening of the cloacal chamber and the adjacent glandular

zone. Spines (Fig. 21) are only very slightly or not at all keeled. The color in alcohol is dark gray with a brown tinge. The prothorax is whitish-brown, and the buccal plate is darker and shows three incisions on its dorsal edge of which the median one contains the mouth opening. The muscles are fairly thick, consisting of two pairs each of dorsal and lateral retractors at the front end. In the anterior half of the prothorax there is a characteristic isolated small bundle of longitudinal muscles on both sides of the mid-dorsal line. Gill-retractor muscles are typical. The nervous system is also typical, with a brain situated very near the

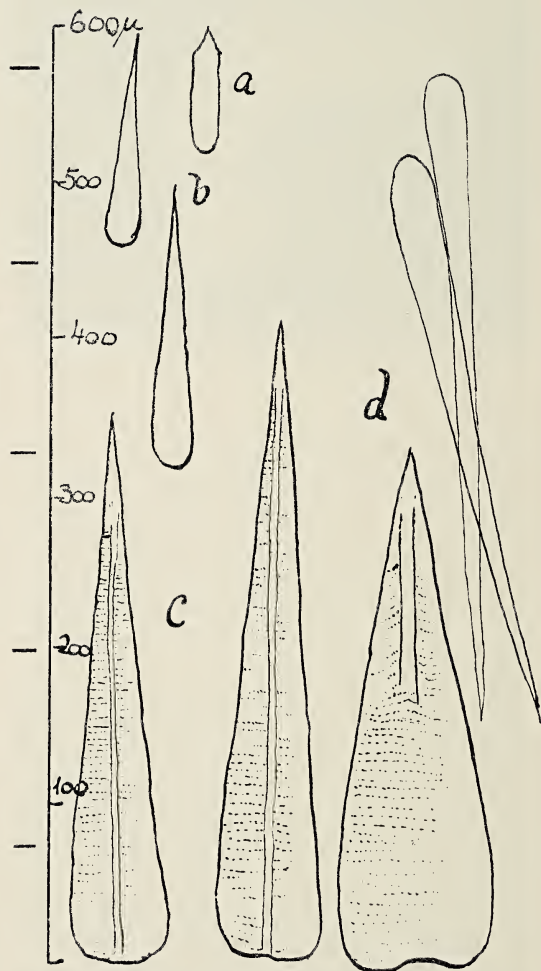


FIG. 23. *Crystallophrisson marinellii*. Characteristic spicules from body regions a, b, c, and d.

anterior end of the body, with three pairs of precerebral ganglia, and the cerebrobuccal connective split off the common trunk immediately after leaving the brain. The fore-gut is short and unusually wide, with small lateral folds occurring only in the radular region. The buccal glands are in front of the sphincter muscle, and all three kinds of salivary glands are present, the lateral ones being notably large and surrounding also the junction of mid- and fore-gut. The radula is characteristic, large, and lacking real teeth; the tongue has a very stout, highly chitinous cuticle which on either side of the median toothlike structure may attain a thickness of 25 μ . The mid-gut is narrow. The liver has granular cells on the dorsal wall and on the edge of the numerous septa.

Reproductive organs are typical; the openings of the gonoducts are on papillae, their epithelium not continued on the wall of the cloacal chamber. The pericardium is very spacious and extends far backward; the ventricle is highly muscular, and there are two atrio-ventricular openings.

DISTRIBUTION: Five specimens, all from the San Pedro area of southern California, come from depths of 415–430 fm, in mud.

Crystallophrisson marinellii n. sp.

Figs. 23, 24

COLLECTIONS:

- 2363 (1) in 429 fm, with *Prochaetoderma californicum* and *C. sp.*
 2473 (1) in 16 fm.
 2753 (1) in 322 fm.
 2884 (1) in 190 fm.

DIAGNOSIS: This is a comparatively large specimen (Fig. 24), measuring from 20–40 mm long in a state of contraction; the greatest width is 3 mm in the region of the pinkish-white prothorax which may attain a length of 5–7 mm. The terminal buccal plate is brown and rounded in shape. It has a single deep cleft on its dorsal side which contains the wide mouth opening. In alcohol the body is gray with a distinct pink shade. The spines (Fig. 23) are large but weak, and have a slight keel; abdominal spines are very short. The dorso-terminal sense organ is covered with small

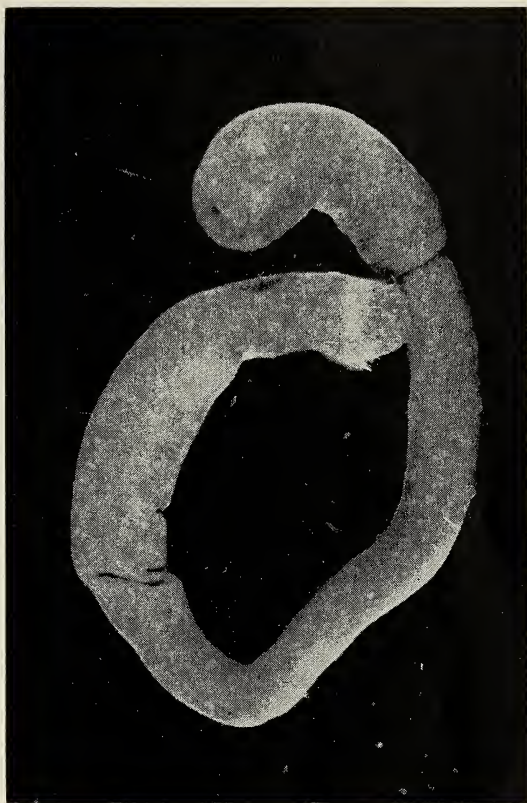


FIG. 24. *Crystallophrisson marinellii*. Sta. 2884.

spines. It is continuous with the opening of the cloacal chamber in front of which is found a glandular region. Except for the six pairs of very strong gill retractors, the muscles are weak. The longitudinal ones in the prothorax region are split up gradually into numerous bundles. Two pairs of dorsal and several pairs of lateral and ventral retractor muscles are present.

The brain is located near the radular region and is not attached to the dorsal wall of the fore-gut but is surrounded by numerous groups of piriform gland cells belonging to the glands of the buccal plate. The common trunk of the three large connectives follows its course for some distance before the buccal connective is free. Four pairs of precerebral ganglia are present. The suprarectal ganglion may be surrounded by the pericardium and even by the atrium. Behind the mouth opening the fore-gut narrows conspicuously and does not widen

much along its course. The radula is powerful but without real teeth or denticles. All three kinds of salivary glands are present. Buccal glands occur only in front of the sphincter muscle. The mid-gut is very wide. The pericardium is notably large, the ventricle highly muscular and there are two atrioventricular openings. The dorsal vessel originates as a conspicuous ampulla situated in the pericardium.

Reproductive organs are without peculiarity. The ciliated portion of the gonoduct is rather long; the gonoduct openings are on papillae, their epithelium not continued on the wall of the cloacal chamber.

DISTRIBUTION: Four specimens, all from the San Pedro area of southern California, were taken in depths of 16–429 fm, in mud or sandy mud.

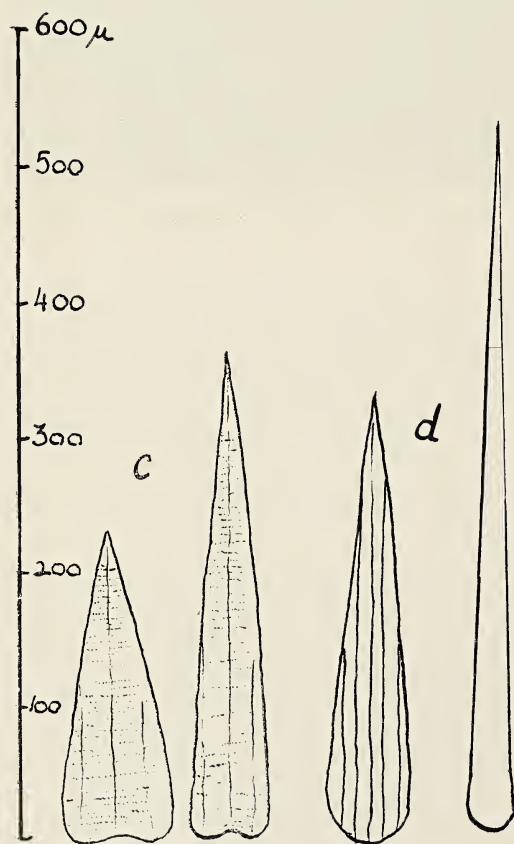


FIG. 25. *Crystallophrisson rectum*. Characteristic spicules from body regions *c* and *d*.



FIG. 26. *Crystallophrisson rectum*. Sta. 2798.

Crystallophrisson rectum n. sp.

Figs. 25, 26

COLLECTIONS:

2644 (1) in 310 fm, with *Limifossor fratula* and *C. hartmani*.

2798 (1) in 386 fm, with *Prochaetoderma californicum* and *C. hartmani*.

DIAGNOSIS: These animals are moderately large (Fig. 26) being 10–18 mm long, and having an average diameter of 1–1.5 mm. The prothorax may reach 2.5 mm in diameter. The color is yellowish-brown. The spines (Fig. 25) are weak and have little structure. The buccal plate is semicircular and has a deep and wide dorsal cleft which contains the mouth opening. The cuticle is very thin, the abdominal gland zone present. The subepidermal muscle layers are weak; there are three pairs of dorsal, three pairs of lateral, and several pairs of ventral

retractor muscles. Only five pairs of gill retractors are present; the ventral posterior ones are lacking.

The nervous system shows a very compact mass of three pairs of precerebral ganglia and a markedly bilobed brain, both attached to the dorsal wall of the fore-gut; the buccal nerve is shortly freed. The supraectal ganglion is surrounded by the pericardium. The fore-gut is narrow, triangular in outline where located

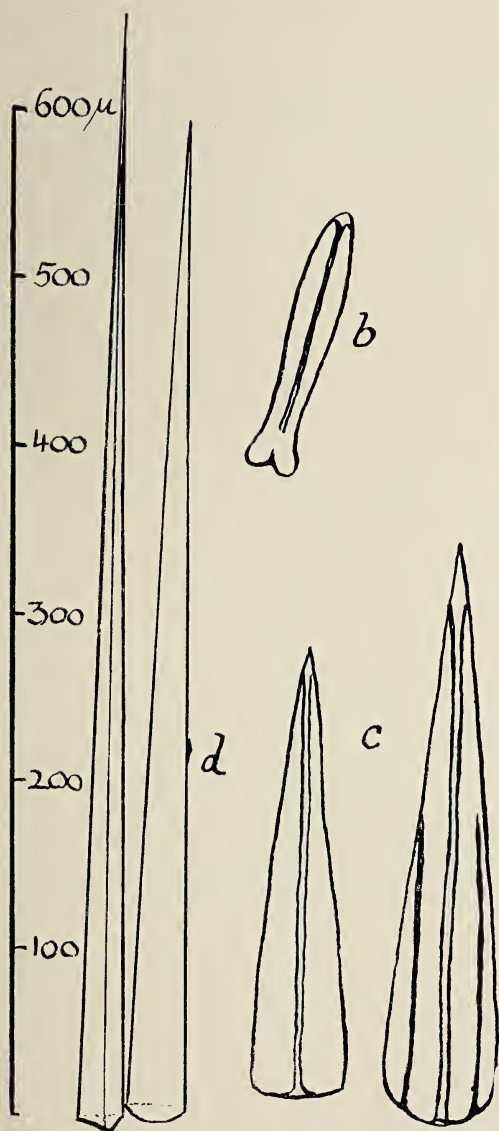


FIG. 27. *Crystallophrisson rubrum*. Characteristic spicules from body regions *b*, *c*, and *d*.



FIG. 28. *Crystallophrisson rubrum*. Sta. 2150.

between the mouth opening and the brain, then semicircular in the brain region, and somewhat widened and quadrangular in the region of the radula. Numerous buccal glands are visible behind the sphincter and all three kinds of salivary glands are present. The radula is typical and lacks denticles. The mid-gut is wide and has a cuticular region near its opening to the liver. The rectum is slightly winding.

The pericardium is spacious, the ventricle slender and not very muscular, with two atrio-ventricular openings. The dorsal vessel begins with a bulb. Gills are conspicuously small and have only a few gill lamellae. The epithelium of the gonoducts is not continued on the wall of the cloacal chamber.

DISTRIBUTION: Two specimens come from the San Pedro area, southern California, in 310–386 fm, one from clay sediments, the other from mud with glass sponge.

Crystallophrisson rubrum n. sp.

Figs. 27, 28

COLLECTION:

2150 (1) in 310 fm, with *C. hartmani* and *C. riedli*.

DIAGNOSIS: This species is readily distinguished from others by its outer purple color and its plump body (Fig. 28). The single specimen measured 17 mm long and 2.5 mm at its greatest width. The front end was withdrawn and the exact outline of the buccal plate is thus not known, but it is certainly pierced by the mouth opening. The spines (Fig. 27) are large and stout and have a distinct keel; the abdominal needle-like spines attain a length of 800 μ . A glandular zone in front of the opening of the cloacal chamber is present and "giant cells" are frequently encountered in the epidermis of the entire body. The animal is highly muscular; there are two pairs of dorsal, one pair of lateral, and one pair of ventral retractors of the front region, all of them very strong. These retractors split off from the longitudinal muscle layer which is located dorsally in the prothorax, dividing only into a few rather large bundles. The six pairs of gill-retractor muscles are typical; the anterior dorsal one has a double origin. The diaphragms are very strong, and an anterior vertical one can be distinguished.

The nervous system shows three pairs of small compact precerebral ganglia, a small brain, separated from the dorsal wall of the fore-gut by a large sinus, and a cerebrobuccal connective split off the common trunk at some distance from the latter's origin. The fore-gut is provided with strong longitudinal muscle fibres and with a stout sphincter, with buccal glands anterior to the last and with all three kinds of salivary glands, of which the dorsal ones open into an unusually large pouch of the fore-gut. The strong radula consists of the typical parts in addition to a pair of small pointed, curved denticles.

The reproductive organs are typical; the gonoducts are simple without sacculations; their dorsal ciliated parts are long and slender tubes. The epithelium of their outlets continues on the wall of the cloacal chamber. The

pericardium is very large and together with the posterior part of the atrium surrounds the suprarectal ganglion. The muscular ventricle, connected with the atrium by two atrioventricular openings, is attached at its front end to the dorsal and ventral pericardial wall. The dorsal vessel begins as a large bulb.

DISTRIBUTION: This species is known through a single specimen from Redondo canyon, in the San Pedro area, southern California, in 310 fm, in mud.

ACKNOWLEDGMENTS

The author is indebted to all those who made these collections possible. The operations of the "Velero IV" were supported by funds provided partly by the Allan Hancock Foundation, the California State Water Pollution Control Board, and the National Science Foundation. The sorting of solenogasters was done by staff members of the Hancock Foundation; the anatomical preparations were prepared in the laboratory of the Department of Zoology, University of Vienna. The author is also indebted to the Austrian Department of Education and the Department of Zoology of the Free University of West Berlin.

APPENDIX

ADDITIONAL STATION DATA

Physical data are published for most of the station numbers listed above. Those not separately listed below are to be found in Hartman (1955) and Hartman and Barnard (1958, 1960). The following are newly listed; all localities are in southern California.

2457-53. Oct. 17, 1953. 4.0 miles SE of Point Fermin lighthouse, 33° 39' 19" N. lat., 118° 14' 20" W. long. In 21.5 fm. A snapper sampler took a very small sample of sand.

2884-54. July 27, 1954. 5.6 miles SW of end of Newport pier. 33° 31' 58" N., 118° 00' 00" W. In 190 fm. The orange-peel-grab took 1.93 cu ft of gray green mud.

2888-54. July 27, 1954. 14.7 miles EWE of East end, Santa Catalina Island. $33^{\circ} 21' 58''$ N., $118^{\circ} 02' 00''$ W. In 390 fm. OPG took 2.67 cu ft of gray green mud.

2895-54. July 28, 1954. 9.9 miles SSW of end of Newport pier. $33^{\circ} 27' 57''$ N., $118^{\circ} 01' 58''$ W. In 265 fm. OPG took 2.58 cu ft of gray green mud.

2899-54. July 28, 1954. 8.25 miles SW of end of Newport pier. $33^{\circ} 30' 00''$ N., $118^{\circ} 02' 02''$ W. In 266 fm. OPG took 2.64 cu ft of gray green mud.

2901-54. Aug. 11, 1954. 12.8 miles SW of East end, Santa Catalina Island. $33^{\circ} 26' 00''$ N., $118^{\circ} 06' 06''$ W. In 312 fm. OPG took 3.02 cu ft gray green mud.

3037-55. May 8, 1955. 3.75 miles from North light, Santa Barbara Island. $33^{\circ} 31' 17''$ N., $118^{\circ} 58' 00''$ W. In 360 fm. OPG took 2.58 cu ft of gray green sandy mud.

3204-55. July 7, 1955. Santa Monica Bay. $33^{\circ} 58' 10''$ N., $118^{\circ} 39' 10''$ W. In 115 fm. OPG took 2.08 cu ft of green silty mud.

3205-55. July 7, 1955. Santa Monica Bay. $33^{\circ} 58' 00''$ N., $118^{\circ} 37' 00''$ W. In 88 fm. OPG took 2.08 cu ft of green silty mud.

4756-56. Dec. 8, 1956. 4.1 miles from Scripps pier, La Jolla. $32^{\circ} 51' 55''$ N., $117^{\circ} 20' 30''$ W. In 102 fm. OPG took 2.39 cu ft of green mud and some broken shells; temperature of sediment 9.8 C.

4776-56. Dec. 10, 1956. 2.2 miles from Dana Point. $33^{\circ} 26' 00''$ N., $117^{\circ} 43' 30''$ W. In 87 fm. OPG took 3.46 cu ft of green mud; temperature of sediment 10.2 C.

4778-56. Dec. 10, 1956. 5.2 miles from Dana Point. $33^{\circ} 30' 20''$ N., $117^{\circ} 47' 45''$ W. In 100 fm. OPG took 2.96 cu ft of green mud. Temperature of sediment 9.7 C.

4835-57. Feb. 6, 1957. 11 miles from Port Hueneme Light. $34^{\circ} 02' 15''$ N., $119^{\circ} 01' 45''$ W. In 77 fm. OPG took 1.38 cu ft of olive green sandy silt.

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Studies in *Fitchia* (Compositae): Novelties from the Society Islands; Anatomical Studies

SHERWIN CARLQUIST and MARTIN L. GRANT¹

THE GENUS *Fitchia* has attracted interest because of its arborescent habit, its distribution in southeastern Polynesia, the endemism of its species, and its phylogenetic relationships. In a monograph of this genus, six species occurring on five islands were recognized (Carlquist, 1957). Following the appearance of that monograph, Grant notified Carlquist of his collection, while on a Bishop Museum Fellowship in 1931, of specimens of *Fitchia* from two additional islands (Bora Bora and Tahaa) in the Society Group. The genus had not been previously reported from these islands, and manuscript names, as a new species and subspecies, respectively, had been applied to the taxa. On Grant's invitation, Carlquist made the anatomical studies presented here which, it is felt, puts the recognition of the two new entities on a much firmer basis than gross morphology alone could have provided. In addition, descriptions are given of one additional specimen each of two previously known species of *Fitchia*, one from Tahiti, and one from Rapa. The occurrence of the two novelties is of more than ordinary interest because of the nature of this genus, and permits more extended remarks on the nature of speciation in *Fitchia*. Flowering material of *F. rapensis*, not available for the monograph, has been studied here. This paper, therefore, may be considered an addendum to the monograph. The taxonomic descriptions below have been prepared by Grant. The anatomical account which follows is the work of Carlquist, and has been prepared to conform with the types of data offered in the monograph.

TAXONOMIC DESCRIPTIONS

1. *Fitchia cordata* M. L. Grant et S. Carlquist, sp. nov.

Fig. 31

Frutex arboreus 2 m altus glaber, caule basiliter 4 cm crasso. Folia simplicia petiolata petiolis 25–65 mm longis, longitudine media ($N=42$) 47 mm. Laminae late obovatae vel suborbiculares luteovirides 40–72 mm longae 36–65 mm latae, magnitudine media foliarum grandiorum circa 58×54 mm, basi cordata vel rotundata, apice obtuso acutove vel parum acuminato, margine crenulato vel subintegro, venulis lateralibus 5–10 (numero medio 8.5) pro unico latere. Pedunculi terminales 20–40 mm longi, longitudine media ($N=7$) 33 mm. Capitula solitaria circa 40-florata. Involucra 25 mm longa 25 mm lata, bracteis 3–4 seriatis viride-lutei coriaceis marginibus scariosis, exterioribus late triangularis 3 mm longis 9 mm latis, mediocribus semiorbicularibus, interioribus lanceolatis 13–17 mm longis 5–7 mm latis. Bractee receptaculares 12–17 mm longae 2–3 (–5) mm latae. Corollae 15–20 mm longae, tubis circa 10 mm longis, sinibus subaequalis. Antherae saccis 5 mm longis, apicibus staminum cuneato-lanceolatis 1–1.5 mm longis. Ovaria ad anthesin 7–8 mm longa, stylis 20–22 mm longis. Achaenia matura 13–16 mm longa, aristis 8–10 mm longis plerumque triangularis in sectione transversa subdeciduis.

Tree-like shrub, 2 m tall, 4 cm in diameter at the base, glabrous. Bark 1 mm thick, brown, almost smooth, with fine longitudinal ridges 0.5 mm deep. One-year twigs on flowering shoots greenish, 2.5–3 mm in diameter; two-

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FIGS. 1–6. Secondary xylem. Figs. 1–4, *Fitchia cuneata* ssp. *tabaaensis*. Figs. 5–6, *F. cordata*. Figs. 1, 2: Transverse sections; note tyloses in vessels; Fig. 2, a sclerified tylosis in which the lumen is nearly occluded. Figs. 3, 4: Tangential sections; Fig. 3 is a portion showing long, thick-walled fibers; Fig. 4 shows storied apotracheal parenchyma cells. Fig. 5: Transverse section; note band of apotracheal parenchyma above center of photograph. Fig. 6: Tangential section. Fig. 2, $\times 300$; others, $\times 117$.

year twigs pale brown, 4–5 mm in diameter; internodes 4–12 mm long, on vegetative shoots to 20 mm long. Leaves simple. Petioles 25–65 mm long, the average being 47 mm ($N=42$); the stipular sheaths 0.4–0.6 mm high. Blades

broadly ovate to suborbicular, yellowish-green, with a narrow (0.3 mm) stramineous margin, and with a dark callous at the apex; 40–72 mm long, 36–65 mm wide, the average ($N=8$) size of the largest blade on the flowering shoots

being 62×55 mm, the second largest 58×54 mm, and the smallest of the fully-developed leaves 64×43 mm; the base cordate to a depth of 1–2 (–3) mm or rounded; the apex obtuse to acute, with the margins near the tip slightly rounded to straight, or, if barely acuminate, departing at most 1 mm from a straight line; the margin crenulate, with 2–3 indentations (up to 0.5 mm deep) per cm, to subentire, the base entire for 20 mm adjacent to the petiole; with 5–10 (average 8.5) pairs of major lateral veins, usually curving somewhat towards the tip of the leaf. Peduncles terminal, 20–40 mm long, the average ($N=7$) 33 mm, often arcuate and reflexed. Head solitary, with about 40 flowers. Involucres 25 mm long and 25 mm wide; the bracts in 3–4 series, greenish-yellow, coriaceous, scarious-margined, the outermost broadly deltoid (3 mm long, 9 mm wide), the middle ones semicircular, and the inner ones lanceolate (13–17 mm long, 5–7 mm wide). Receptacular bracts 12–17 mm long, 2–3 (–5) mm wide. Corollas 15–20 mm long, the tube about 10 mm long, the shallower sinuses nearly equalling the ventral cleft, and the lobes with terminal hairs 0.1–0.6 mm long. Anther sacs 5 mm long, the stamen tips cuneate-lanceolate, 1–1.5 mm long. Ovary at anthesis 7–8 mm long; the styles 20–22 mm long. Ripe achenes 13–16 mm long, with awns 8–10 mm long; awns generally triangular in transection and somewhat deciduous.

DISTRIBUTION: Society Islands, endemic to Bora Bora.

SPECIMEN EXAMINED: Bora Bora, in dwarf rain-forest on the summit of Mt. Tarapaia, altitude 645 m, Jan. 3, 1931, *M. L. Grant* 4968 (BISH, type; RSA, ISTC, isotypes).

This species was found in several places on Mt. Tarapaia, none less than 25 m in altitude below the summit, but only four inflorescences were discovered, two in bud, one at anthesis, and one in fruit. Associated woody plants were *Alstonia*, *Metrosideros*, *Freycinetia*, and *Glochidion*. Native name: anei.

Mt. Tarapaia appears on U. S. Hydrographic maps as Mt. Pahia, elevation 2165 ft (= 660 m), the name and elevation being taken from French maps. It has been recorded as "Tarao-pai'a." The only higher point on Bora Bora is

Otemanu (Mt. Temanu of the maps), elevation 725 m, a peak which apparently has never been climbed by anyone other than Polynesians.

2. *Fitchia cuneata* J. W. Moore, Bishop Mus. Bull. 102:48. 1933 ssp. *tabaaensis* M. L. Grant et S. Carlquist, subsp. nov.

Fig. 32

Frutex arboreus 2.5 m altus glaber, caule basaliter 2.5 cm crasso. Folia simplicia petiolata petiolis 10–37 mm longis, longitudine media ($N=30$) 20 mm. Laminae plerumque ellipticae vel parum ovatae obovataeque vel rhomboidales subatrovirides 40–110 mm longae 25–58 mm latae, magnitudine media foliarum grandiorum circa acuminato, margine crenulato serratove vel subintegro, venulis lateribus 5–10 (numero medio 7.5) pro unico latere. Pedunculi terminales 25–50 mm longi, longitudine media ($N=10$) 33 mm. Capitula solitaria circa 75-florata. Involucra 20–40 mm longa, 15–25 mm lata, bracteis 3–4 seriatis, viridilutei coriaceis marginibus chartaceis, exterioribus breviter ovatis reniformibusque 2–5 mm longis 6–15 mm latis, medioribus semiorbicularibus 8–12 mm longis 9–13 mm latis, interioribus cuneatis 12–20 mm longis, 4–8 mm latis. Bractee receptaculares lanceolatae 12–17 mm longae 2–4 mm latae. Corollae ad anthesin 15–22 mm longae, tubis 4–10 mm longis, dentibus 5–7 mm longis. Antherae saccis, 4.5–5 mm longis, apicibus staminum cuneato-lanceolatis 1.5 mm longis. Ovaria ad anthesin 8–10 mm longa, 3–4 mm lata, stylis 24–30 mm longis. Achaenia matura 10–20 mm longa, 4–6 mm lata, aristis 10–13 mm longis plerumque teretibus subpersistentibus.

Treelike shrub, 2.5 m tall, 2.5 cm in diameter at the base, glabrous. Bark 1 mm thick, brown, roughened with irregular scaly ridges. One-year-old twigs on flowering shoots greenish, 2 mm in diameter; two-year twigs pale brown, 3 mm in diameter; internodes 4–8 mm long, on vegetative shoots to 12 mm long. Leaves simple. Petioles 10–37 mm long, the average ($N=30$) 20 mm; the stipular sheaths 0.5–0.8 mm high. Blades mostly elliptical, varying to slightly ovate, obovate, or rhomboid, dull green, with a narrow stramineous margin, and with a dark

callous at the apex; 40–110 mm long, 25–58 mm wide, the average size ($N=10$) of the largest leaf on flowering shoots 84×45 mm, the second largest 75×42 mm, and the smallest of the fully developed leaves 59×30 mm; the base cuneate (usually) to barely rounded; the apex acute, occasionally slightly acuminate; the margin crenulate to toothed or subentire, with 2–4 indentations (up to 1 mm deep) per cm; with 5–10 (average 7.5) pairs of major lateral veins, mostly curving slightly toward the tip of the leaf. Peduncles terminal, 25–50 mm long, the average ($N=10$) 39 mm long, always reflexed and usually arcuate at anthesis. Heads solitary, with about 75 flowers. Involucres 15–25 mm long, 20–40 mm wide; the bracts in 3–4 series, greenish-yellow, coriaceous, chartaceous-margined, the outermost short ovate or reniform (2–5 mm long, 6–15 mm wide), the middle ones semi-circular (8–12 mm long, 9–13 mm wide), and the inner cuneate (12–20 mm long, 4–8 mm wide). Receptacular bracts lanceolate, 12–17 mm long, 2–4 mm wide. Corollas at anthesis 15–22 mm long, the tube 7–10 mm long, and the teeth 5–7 mm long, the shorter teeth about half the length of the limb, or eventually equalling it; lobes with hairs about 0.75–1 mm long. Anther sacs 4.5–5 mm long, the stamen tips cuneate-lanceolate, 1–1.5 mm long. Ovary at anthesis 8–10 mm long, 3–4 mm wide; styles 22–30 mm long, the stigmatic branches 0.8 mm long, barely separating at anthesis. Mature achenes 10–20 mm long, 4–6 mm wide; the awns 10–13 mm long, generally rounded in transection, subsistent.

DISTRIBUTION: Society Islands, endemic to Tahaa.

SPECIMEN EXAMINED: Tahaa, district of Ruutia, slopes of Mt. Ohiri, in rain-forest of *Crossostylis*, *Alstonia*, and *Morinda*, altitude 465 m, Jan. 25, 1931. *M. L. Grant 5161* (BISH, type; RSA, ISTC, isotypes).

This subspecies was observed in three other nearby localities, all within an altitudinal range of 15 m, and about 70 m below the top of Ohiri, the highest point on the island. Other associated woody plants were *Xylosma*, *Meryta*, *Metrosideros*, *Wikstroemia*, *Fagara*, *Astronia*, and *Hernandia*.

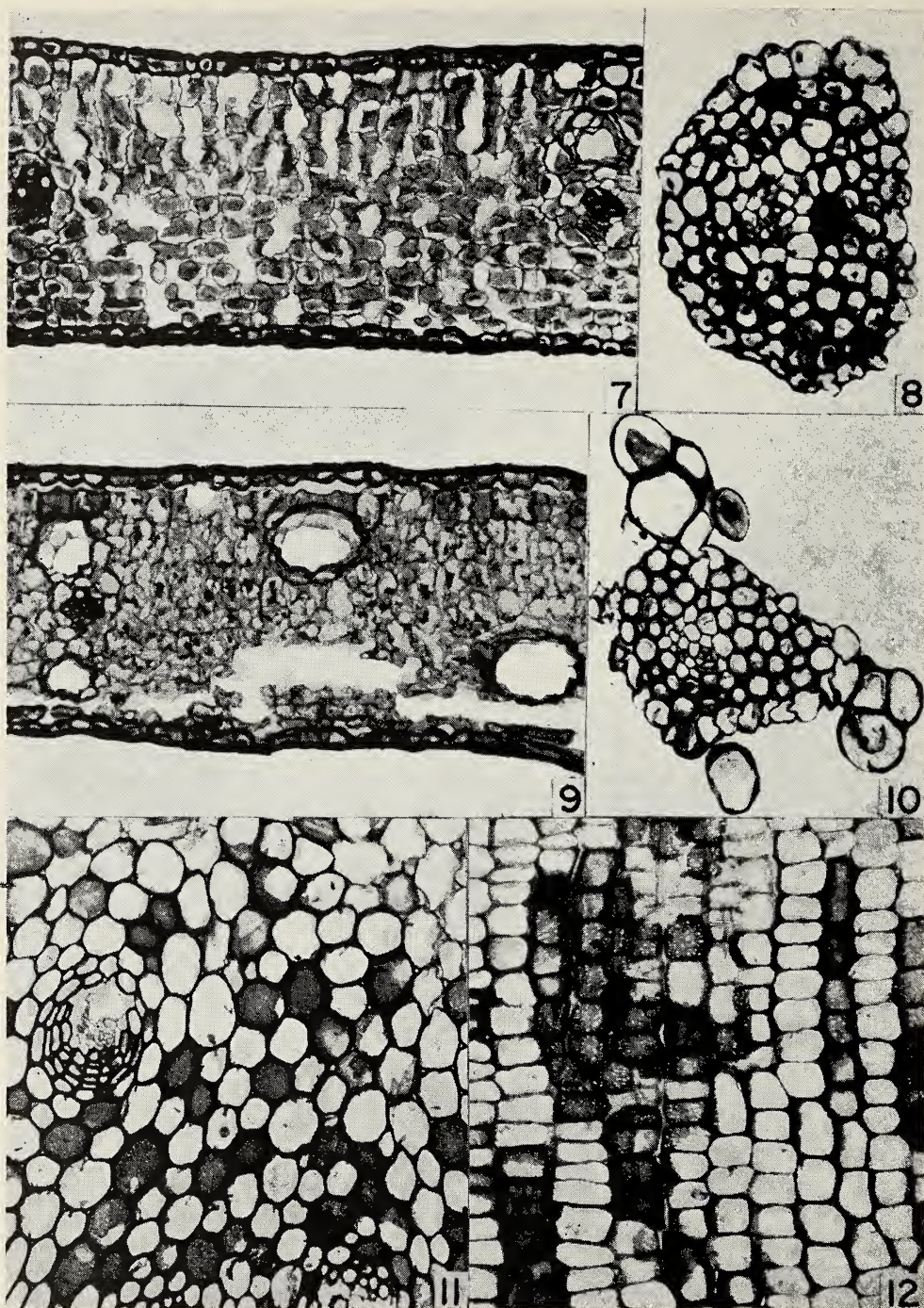
3. *Fitchia nutans* Hook f., London Jour. Bot. 4:640, t.23–24. 1845.

Since so few specimens of this species are available in the United States, and the several Kew and Paris sheets are without detailed habitat data, the citation of an additional collection may be of interest: Tahiti iti, district of Teahupoo, on Mt. Ronui, in *Metrosideros-Weinmannia* forest, altitude 890 m, July 2, 1930, *M. L. Grant 3925* (BISH, ISTC). The following description is from this collection alone.

Trees shaped glabrous shrub, 2.5 m tall, with a basal diameter of 5 cm; bark 2 mm thick, brown, with longitudinal ridges about 1 mm deep; the wood very sweet-smelling. One-year twigs 2–3 mm in diameter; two-year twigs 3.5–4.5 mm thick; internodes 7–10 mm long. Petioles 30–60 mm long; stipular sheaths 2–3 mm high. Blades ovate, yellowish-green, 60–130 mm long, 45–80 mm wide, the average of 12 leaves being 96×61 mm; truncate or cordate at the base, occasionally barely rounded, often somewhat oblique; the apex slightly acuminate; the margin irregularly and shallowly crenulate to entire; with 8–10 major lateral veins. Peduncles two in each of the four inflorescences present, 60–65 mm long, reflexed. Heads shattered with age, the involucral bracts and corollas having dropped. Receptacular bracts 13–14 mm long, 3–5 mm wide. Ripe achenes 9–10 mm long, 2–2.5 mm wide, with persistent awns 7–8 mm long.

This collection fits the general description of the species (Carlquist, 1957: 63), except as follows, with Carlquist's measurements and notes in parentheses: plant smaller (4.5–7.5 m tall), blades often crenulate (entire), maximum leaf size greater (115×70 mm), base often truncate to cordate (acute to obtuse), heads paired (solitary), receptacular bracts shorter (20–22 mm long), achenes much shorter (16–17 mm long at anthesis) and narrower (3–4 mm). These differences, however, do not seem significant enough to warrant separation, and the material matches Hooker's plate closely.

Although the type of the species was supposedly from "Elizabeth Island," all the evidence (Carlquist, 1957: 63) suggests that it is confined to Tahiti. The present specimen comes



FIGS. 7-12. Figs. 7, 8, 11, *Fitchia cordata*. Figs. 9, 10, 12, *F. cuneata* ssp. *tabaaensis*. Fig. 7: Leaf transection, adaxial face above. Secretory canal is above vein at right. Fig. 8: Transection of awn from an achene, adaxial face at right. Note lignification of hypodermal layers, presence of a single vascular bundle. Fig. 9: Leaf transection, adaxial face above. In addition to secretory canals adjacent to vein, left, secretory cavities may be seen, center and right. Fig. 10: Transection of awn from an achene, adaxial face upper right. Trichomes in section, above and below. Fig. 11: Transection of pith. Secretory canal with adjacent fibrosclereids, above; inner margins of vascular cylinder, below; note thin-walled cells at top of figure. Fig. 12: Longitudinal section of pith. All cells have secondary walls, some such are thicker walled. Figs. 7, 9, $\times 145$. Figs. 8, 10, $\times 255$. Figs. 11, 12, $\times 135$.

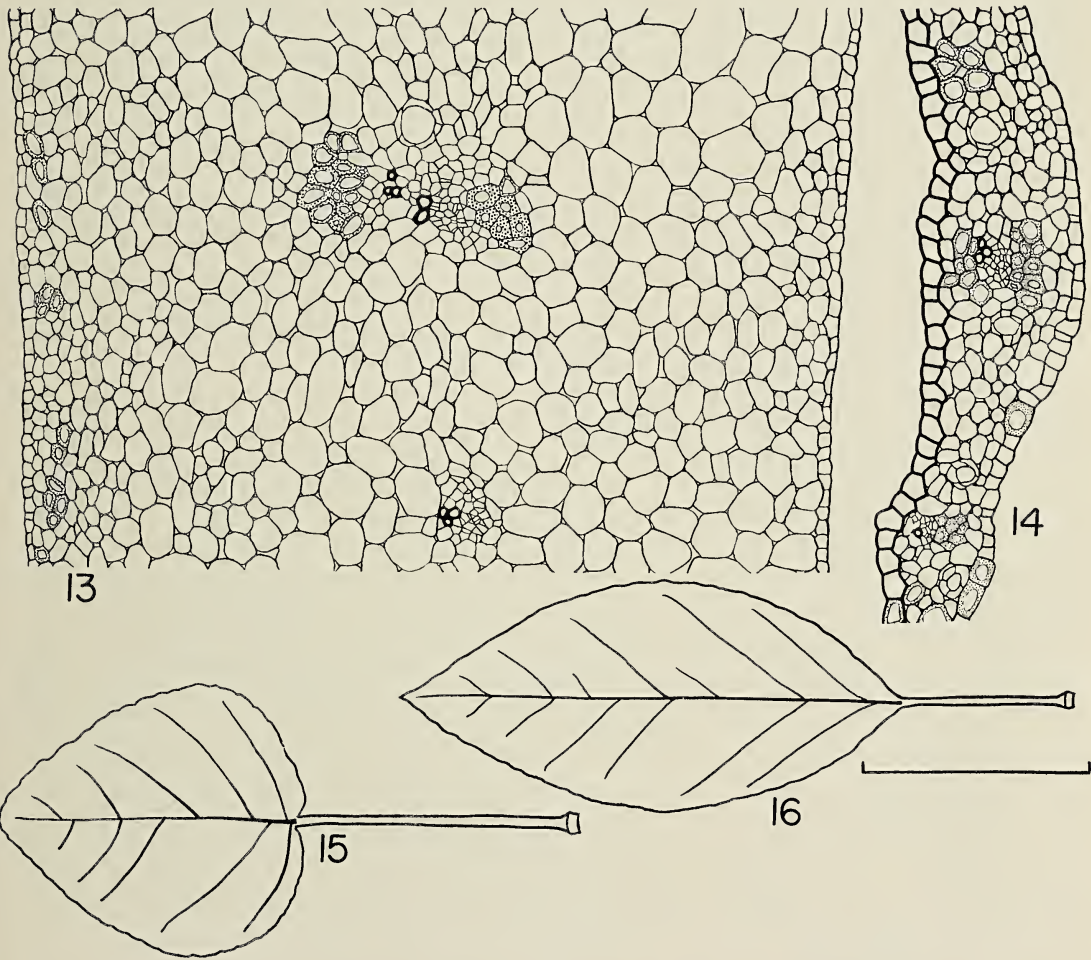
from the smaller mountain (Tahiti-iti) of the two which make up the island.

Hoffmann (1890: 353) reported *F. nutans* from Tabuai (= Tubuai), as well as from Tahiti and Elizabeth (now Henderson) I., but as Hemsley (1885: 20) had earlier shown, this supposed locality is based on the type sheet (Cuming 1424) which Hooker had earlier attributed to Elizabeth Island.

Erdtman (1952: 124) cites a specimen of *F. nutans* as "Fiji, Moseley, anno 1875." Carlquist (1957:63) suggested that this is in error,

because no other collections have been made of *Fitchia* in the Fiji group. Also, Hemsley (1885: 20) reports that there is at Kew a specimen collected by Moseley in Tahiti at an altitude of 4,000 ft, and this is probably the specimen cited by Erdtman.

Papy (1955: 325) mentions *F. nutans* as growing on "Tahiti, Moorea, Raiatea, Rapa." The record from Rapa is probably based on the report of Riley (1926: 55), which was made before *F. rapensis* had been described as a separate species (Brown, 1935: 366), although



FIGS. 13-16. Fig. 13: *Fitchia cordata*. Transection of involucre bract taken about midway along length of bract; adaxial face at left. Fig. 14: *F. cordata*. Transection receptacular bract, adaxial face at left. In Figs. 13, 14, tracheary elements shown in bold outline, fibers and sclereids stippled. Fig. 15: "Typical" leaf of *F. cordata*, showing main veins. Fig. 16: "Typical" leaf of *F. cuneata* ssp. *tabakaensis*. Figs. 13, 14, $\times 105$. Figs. 15, 16, $\times 2\frac{1}{2}$.

Papy was aware of this. Neither Moore nor Grant found *F. nutans* on Raiatea, and Papy was aware of the description of *F. cuneata* from that island. Moorea is certainly a likely locality for *F. nutans*, but for none of these localities does Papy cite specimens.

Thus, the geographic distribution offered by Carlquist (1957:2) must be broadened to include the occurrence of *F. nutans* on Tahiti-iti, *F. cordata* on Bora Bora, and *F. cuneata* ssp. *tabaaensis* on Tahaa.

4. *Fitchia rapensis* F. Brown, Bishop Mus. Bull. 130:366. 1935.

Since the ten previously recorded collections of this species are all without flowers (Carlquist, 1957: 62), the description of a flowering specimen should be of interest: Rapa, moist zone, altitude 520 m, Jan. 3, 1922, W. B. Jones 372 (Whitney Expedition) (BKL).

"Tree," glabrous. Petioles 40–75 mm long. Blades ovate, the larger ones averaging 90 mm long and 84 mm wide, rounded or scarcely cuneate at the base, the apex acute; entire; with about 12 pairs of major lateral veins. The single inflorescence is terminal, with two heads, the peduncles 50 and 60 mm long, reflexed. Heads 45 mm long and 45 mm wide. Bracts in about 4 series, those of the second layer semi-circular, 10 mm long and 22 mm wide, and those of the inner layer 20 mm long and 12 mm wide. Receptacular bracts cuneate, 16–17 mm long, 3–4 mm wide. Mature corollas 24–26 mm long, the ventral cleft reaching to 6–8 mm of the base, the segments eventually separating to within 10 mm of the base; the tips of the lobes often densely covered with sclerified cells, which are up to 0.75 mm long. Anther sacs 5.5–6 mm long, caudate, the tail 0.3–0.4 mm long; the stamen tips cuneate, 1.5 mm long. Mature style (broken off) at least 32 mm long. Achenes, at and just after anthesis, 10–12 mm long, 4 mm wide, the awns 12–15 mm long, strongly bent and twisted at the base.

ANATOMICAL DESCRIPTIONS

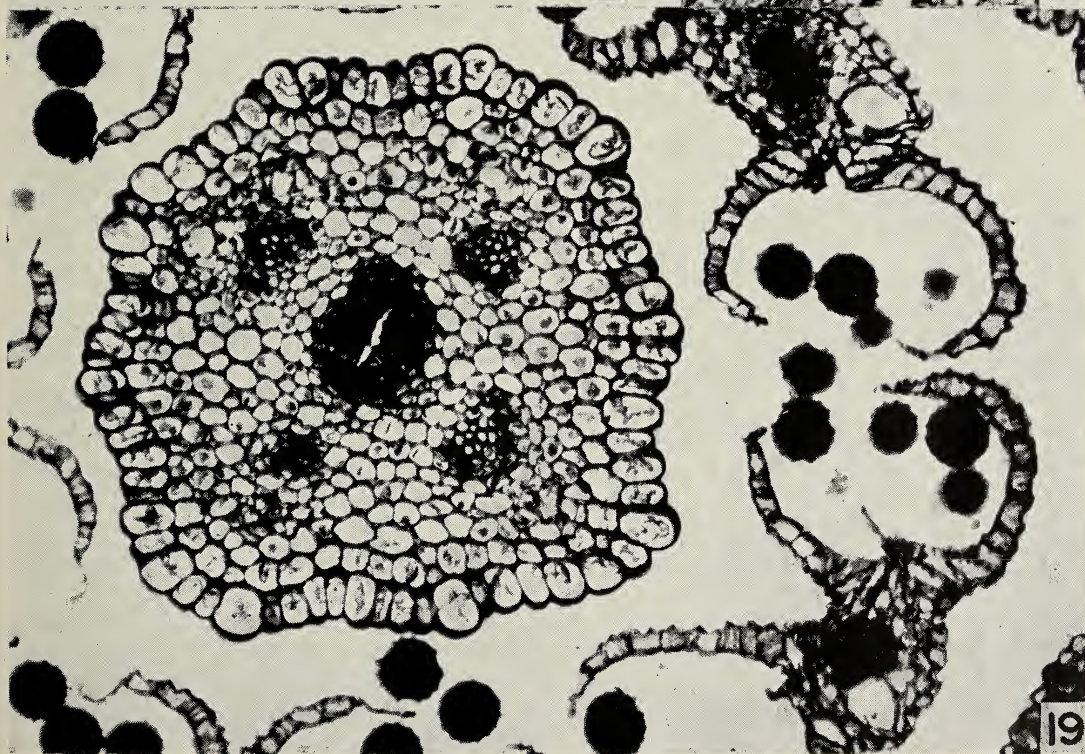
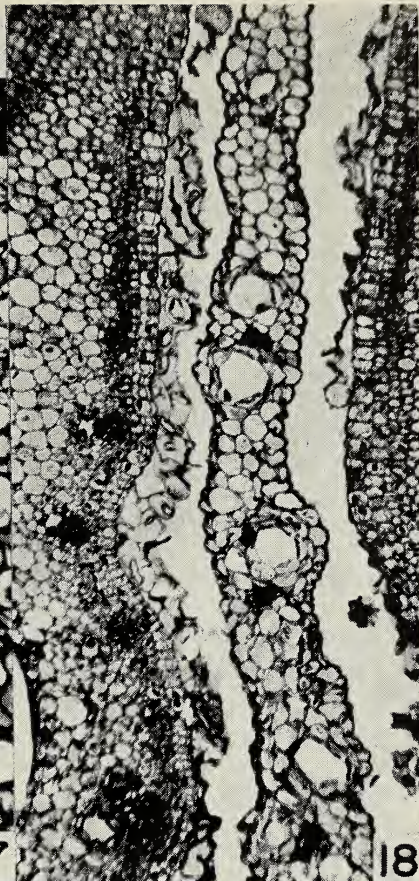
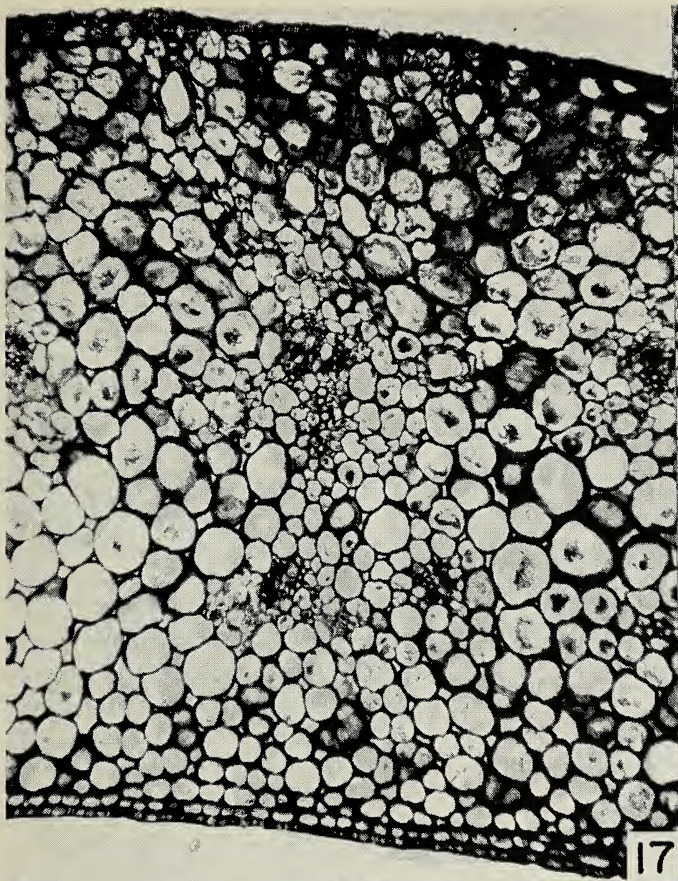
Anatomical studies were based on the herbarium specimens cited above. Liquid-preserved heads of *F. cuneata* ssp. *tabaaensis* and wood samples of both *F. cuneata* ssp. *tabaaensis* and *F. cordata*, for which the herbarium specimens serve as vouchers, were available. The methods of preparation of these materials are the same as those employed for such materials in the two papers (Carlquist, 1957, 1958) dealing with the anatomy of this genus.

SECONDARY XYLEM: With respect to qualitative features, the species of *Fitchia* other than *F. speciosa* are much alike in wood anatomy (Carlquist, 1958). *Fitchia cuneata* ssp. *tabaaensis* and *F. cordata* share the qualitative features of those species. The bands of apotracheal parenchyma are clearly shown by the two new taxa (Figs. 4, 5). Thick-walled fibers are readily apparent in *F. cuneata* ssp. *tabaaensis* (Figs. 1, 3); libriform fibers are less thick-walled in *F. cordata* (Figs. 5, 6). Sclerosed tyloses have been reported in *F. nutans* and *F. speciosa* (Carlquist, 1957, 1958); they are abundant in *F. cuneata* ssp. *tabaaensis* (Figs. 1, 2), although none were observed in *F. cordata*.

Quantitative features of the two new taxa are as follows: *F. cordata*: vessels per group: 1.37; average vessel diameter: 61.5 μ ; diameter of widest vessel: 88 μ ; average length vessel elements: 325 μ ; average length libriform fibers: 502 μ ; average length apotracheal parenchyma cells: 356 μ ; average height multiseriate rays: 1.17 mm. *Fitchia cuneata* ssp. *tabaaensis*: vessels per group: 1.66; average vessel diameter: 62.8 μ ; diameter of widest vessel: 92 μ ; average length vessel elements: 326 μ ; average length libriform fibers: 507 μ ; average length apotracheal parenchyma cells: 380 μ ; average height multiseriate rays: 1.51 mm.

Quantitative as well as qualitative data point up a close similarity between *F. cuneata* ssp. *tabaaensis* and the typical *F. cuneata*. Quantitative and qualitative data for *F. cordata* re-

FIGS. 17–19. *Fitchia cuneata* ssp. *tabaaensis*. Fig. 17: Transection of involucral bract taken about midway along length; adaxial face below. Fig. 18: Transection of receptacular bract; adaxial face and adjacent achene at left. Fig. 19: Transection of style. At center of style, stigmatoid tissue. Exterior to each bundle is a secretory canal, except for bundle at upper left, which is flanked by a pair of canals. At right, anthers in transection. Note secretory canal in each of the two anthers. Fig. 17, $\times 100$; Fig. 18, $\times 80$; Fig. 19, $\times 120$.



semble the figures given (Carlquist, 1958: 6-7) for *F. cuneata* and *F. nutans*.

PITH: Pith anatomy proved important in distinguishing species of *Fitchia* (Carlquist, 1957). Likewise, the two new taxa possess characteristics useful for taxonomic purposes. Pith of *F. cordata* (Fig. 11) consists of both thick-walled, lignified, and thin-walled, non-lignified, cells. Secretory canals are present; each is surrounded by an eccentric zone of fibro-sclereids. Although secretory canals surrounded by small lignified thick-walled cells occur in *F. nutans* and *F. tabitensis*, the presence of these combined with occurrence of thin-walled non-lignified cells in pith is characteristic only of *F. cordata*. Pith of *F. cuneata* ssp. *tabaaensis* (Fig. 12) lacks secretory canals and consists of thin-walled and thick-walled lignified cells. The only pith pattern which matches this is that described in the monograph for typical *F. cuneata*.

LEAF: Leaf dimensions are mentioned in the taxonomic description above. However, averages of dimensions of leaves from a collection were used in the monograph, and these may be compared with those of the new taxa. Mature leaves of the collection of *F. cordata* (Fig. 15) show an average lamina width of 52.5 mm, an average lamina length of 53 mm, and a petiole length of 49.7 mm. The only *Fitchia* which resembles *F. cordata* both in form and dimensions is the extreme population of *F. rapensis* from the summit of Rapa. Leaves of *F. cordata* have longer petioles than that collection, and there is certainly no close relationship between *F. cordata* and *F. rapensis*. Leaves of *F. cuneata* ssp. *tabaaensis* (Fig. 16) which could be termed mature show the following average dimensions: lamina width, 48.0 mm; lamina length, 87.5 mm; petiole length, 26 mm. When compared with the chart in the monograph (Carlquist, 1957: 50) the lamina dimensions fall in the vicinity of *F. nutans* and some collections of *F. rapensis*. The leaves are wider than those of *F. tabitensis* but longer than those of the typical *F. cuneata*. Thus, leaf shape distinguishes both *F. cordata* and *F. cuneata* ssp. *tabaaensis*.

Histological features of leaves of the new taxa also distinguish them. *Fitchia cordata* possesses fibers in bundle sheaths of many veins,

but they are lacking in sheaths of finer veinlets. No secretory cavities are present in the mesophyll, although secretory canals occur adaxially or abaxially to the veins, or both (Fig. 7). Mesophyll is about 10 layers thick. These characteristics are not matched by any other *Fitchia* collection. Presence of a few fibers would ally *F. cordata* to *F. nutans* or *F. tabitensis*, but these two species possess secretory cavities. Absence of secretory cavities does characterize *F. speciosa* and the typical *F. cuneata*, but these taxa lack sclerenchyma in bundle sheaths.

Leaves of *F. cuneata* ssp. *tabaaensis* (Fig. 9) lack sclerenchyma along all but the largest veins. In addition to the secretory canals above and below veins (Fig. 9, left), secretory cavities are present in the mesophyll (Fig. 9, right). The mesophyll is about 10 cells thick. This description agrees closely with that of typical *F. cuneata* except for the presence of secretory cavities. Although such a difference might conceivably arise from a difference in maturity of a plant, it seems more likely a valid difference, for specimens of both subspecies were of flowering age.

INVOLUCRE: The heads of *F. cordata* are small, and the involucre of a living specimen would probably measure about 2 cm in diameter—the smallest involucre size in the genus except for *F. tabitensis* and *F. cuneata*. Involucral bracts of *F. cordata* (Fig. 13) have a thickness comparable to some bracts of *F. nutans*, but differ in their lack of the abundant sclerenchyma which characterizes bracts of *F. nutans*. The mature state of the bracts of *F. cordata* illustrated is certain, because they came from a head in fruit which was in the process of shattering. Occasional lignified thick-walled cells may be seen along the inner face of the bract and around the larger veins. In presence of sclerenchyma and other histological characteristics, the involucral bracts of *F. cordata* are midway between those of *F. nutans* and *F. cuneata*. The receptacular bracts of *F. cordata* (Fig. 14) show similar characteristics. As might be expected, lignified thick-walled cells are more frequent than in the involucral bracts.

Fitchia cuneata ssp. *tabaaensis* also has very narrow involucres, like those of the typical *F. cuneata* or *F. tabitensis*. Histologically, involu-



FIGS. 20–24. Figs. 20, 23, *Fitchia cordata*. Figs. 21, 22, 24, *F. cuneata* ssp. *tahaaensis*. Figs. 20, 21: Tips of corolla lobes, showing exterior surface. Sclerenchymatous cells are shown in black. Figs. 22, 23: Stamen tips, showing inner surface. Anther sacs shown in outline, below. Fig. 24: Base of anther and adjacent filament. Note caudate anther sac, right. All, $\times 65$.

cral bracts of *F. cuneata* ssp. *tabaaensis* (Fig. 17) resemble closely the description given for typical *F. cuneata* in the monograph. This resemblance is especially evident in the lack of sclerenchyma. Only an occasional lignified cell (usually near a vein) can be found. Collenchymatic thickening may occur near outer or inner faces of the bract. In the section shown, more than a single series of bundles may be seen; some of these bundles have distorted orientation of xylem and phloem, a condition mentioned in the monograph for *F. speciosa*. This condition is probably occasional among larger bracts of several species. The thickness of the involucre bract, as well as its lack of sclerenchyma, identifies the two subspecies of *F. cuneata* closely with each other. The receptacular bract (Fig. 18) of a head at anthesis certainly lacks sclereids, although a greater degree of lignification might be apparent in bracts of a head in fruit.

ACHENES: Awn shape and anatomy proved useful characteristics in distinguishing species of *Fitchia*. In comparing illustrations of these (Carlquist, 1957: plate 8) with these of the new taxa (Figs. 8, 10) this also proves to be true. In *F. cordata* (Fig. 8), the awns tend to be rounded in transectional shape, like those of *F. nutans*. However, they show a tendency to be wider than those of *F. nutans*. They have a single vascular bundle and, unlike at least some awns of *F. nutans*, they lack a secretory canal. Awns of *F. cuneata* ssp. *tabaaensis* (Fig. 10) are like those figured for the typical *F. cuneata* in all respects. Presence of three longitudinal zones of trichomes tends to make them triangular as seen in transectional view. Where such trichomes are absent, awns may have a more rounded shape.

COROLLA: In the monograph, considerable attention was focused on the importance of venation patterns of *Fitchia* corollas, both for their phylogenetic importance within Compositae and for their usefulness in distinguishing species. Corolla venation patterns are not illustrated here for the new taxa because they contribute relatively few novel features and can be referred to patterns illustrated in the monograph. Although few flowers of *F. cordata* could be studied in this respect (on account of the

ravages of the living plant by insects), the venation pattern of this species is substantially like that figured for *F. cuneata* or *F. tabitensis*. There is some variation in the levels at which adjacent lateral veins in each lobe join beneath sinuses, but differences in these levels are not nearly so extreme as the condition figured for *F. nutans* (Carlquist, 1957: 10). In their relatively short length (ca. 18 mm) the corollas of *F. cordata* approximate those of *F. tabitensis* also.

Corollas of *F. cuneata* ssp. *tabaaensis* have similar size and venation features. Typically, the patterns are the same as mentioned for *F. cordata*. However, occasionally a pair of adjacent laterals do not join beneath a sinus, but continue into the tube and achene without joining. This condition does occur occasionally in the other species, such as *F. speciosa*. A feature of interest in the corolla of *F. cuneata* ssp. *tabaaensis* is the presence of one or two supernumerary veins in each lobe. In addition to the median and lateral veins, these fine supernumerary veins may be present for a short distance near the base of the lobe. Such veins were not seen in the typical *F. cuneata*, for which, however, mature corollas were not available. Supernumerary veins are occasional in corollas of *F. speciosa*, and characteristically abundant in those of *F. mangarevensis*.

The occurrence of larger numbers of veins in corollas of *F. mangarevensis* is particularly interesting, since that species is close to *F. rapensis*. Corollas, now available, of *F. rapensis* confirm this relationship in the similarly elaborate venation pattern (Fig. 26). This similarity is shown in the presence of five veins per lobe, rather than three. Such a condition is basic in the construction of the *F. rapensis* corolla, although additional veins or vein fragments may be present. The outermost veins of each lobe fuse at the tips of many corolla lobes. The corolla venation of *F. mangarevensis* (Carlquist, 1957: 14) is somewhat more complicated than this, because although the five-vein condition may be observed in some lobes in that species, additional veins are more frequent. The presence of complex corolla venation in both *F. rapensis* and *F. mangarevensis* is interesting in that it raises the question of how complex

venation may have been present ancestrally in *Fitchia*. Is the more complex condition primitive or a specialization? The question cannot be answered in terms of the data available, and cytological information would be very desirable as a line of supporting evidence.

Distribution of thin-walled and thick-walled trichomes and occurrence of sclereids on corolla-lobe tips have proved useful features in the systematics of *Fitchia*. In the two new taxa these features are also of interest. *Fitchia cordata* (Fig. 21) possesses lobe tips not identical to those of any species previously figured. The frequency of sclereids at the lobe tip is notable. Long multiseriate trichomes, all the cells of which are sclereids, are present. No trichomes composed of nonlignified cells were observed. This condition is most closely matched in the genus only in the new subspecies of *F. cuneata* (Fig. 20). In *F. cuneata* ssp. *tahaaensis* sclereids are rare or absent at the lobe tips. The trichomes are long, multiseriate (rarely uniseriate), and composed wholly of sclereids. This condition is not unlike the condition in typical *F. cuneata*, except that the trichomes in the Tahaa plants are few and long.

The corolla-lobe tips of *F. rapensis* (Fig. 25) are, as might be expected, rather similar to those of *F. mangarevensis* (Carlquist, 1957: 27). They are different in that in *F. rapensis* the sclerified trichomes are slightly longer, in general, and extend farther down the lobe. Occasional thin-walled hairs may be seen on the terminal portion of lobes of *F. rapensis*, but the extremely dense coating of thick-walled lignified trichomes clearly marks this pattern as closest to that of *F. mangarevensis*.

STAMENS: Stamen tips likewise offer taxonomic criteria. The long stamen tips of *F. cordata* (Fig. 23) exceed those of *F. nutans* in size, and are thus the longest of the Society Islands species of *Fitchia*. The stamen tips of *F. cuneata* ssp. *tahaaensis* (Fig. 22) are longer than those of the typical *F. cuneata*, but do not differ markedly from those of *F. tahitensis* or *F. nutans*.

The stamen tips of *F. rapensis* (Fig. 27) are 1.5 mm long, thus matching those of *F. mangarevensis*. This is particularly interesting because the two species are so much alike in this respect and because they have longer stamen

tips than the other species of the genus, with the exception of *F. speciosa*.

A feature of some interest not previously observed is the occurrence of somewhat caudate anther sacs in *F. cuneata* ssp. *tahaaensis* (Fig. 24) and the other taxa of *Fitchia*. In view of Cronquist's (1955) dictum that anthers of Compositae are primitively tailless, this would seem curious, because *Fitchia* possesses so many anatomical and morphological characteristics which appear primitive for the family. Cronquist's dictum, for which no appreciable evidence is adduced, seems highly questionable.

In transection the anthers of *F. cuneata* ssp. *tahaaensis* (Fig. 19) exhibit a feature of interest. One or two secretory canals may be observed in the connective of each anther. This condition occurs sparingly in *F. speciosa*, but was not observed in other species of *Fitchia*. The occurrence of anther secretory canals has been noted in other genera which may be related to *Fitchia*, such as *Petrobium* and *Oparanthus* (Carlquist, 1957).

STYLE: Like the anthers, the style of *F. cuneata* ssp. *tahaaensis* (Fig. 19) seems to exhibit more numerous secretory canals than those of other species of *Fitchia*. One canal (or occasionally a pair) is present exterior to each of the four style bundles. Liquid-preserved material is required for accurate demonstration of this phenomenon. In the only other species for which such material was available, *F. speciosa*, canals were much less abundant in styles (Carlquist, 1957). However, as indicated in the monograph, many other Heliantheae do show abundance of stylar secretory canals.

POLLEN GRAINS: The drawings of pollen grains of *Fitchia* (Figs. 28–30) show some differences in representation compared with those of the monograph. Although the outer sculptured layer (ectosexine) is composed of fine rods and spaces, as illustrated earlier, a lacunose inner sculptured layer (endosexine) has now been observed. The endosexine consists of rods interspersed in large spaces. In addition, an inner and outer layer of nexine (below in each figure) may be distinguished. Size and spine shape are of especial interest, however, in comparison of the species. The markedly blunt spines of *F. cuneata* ssp. *tahaaensis* (Fig. 29)

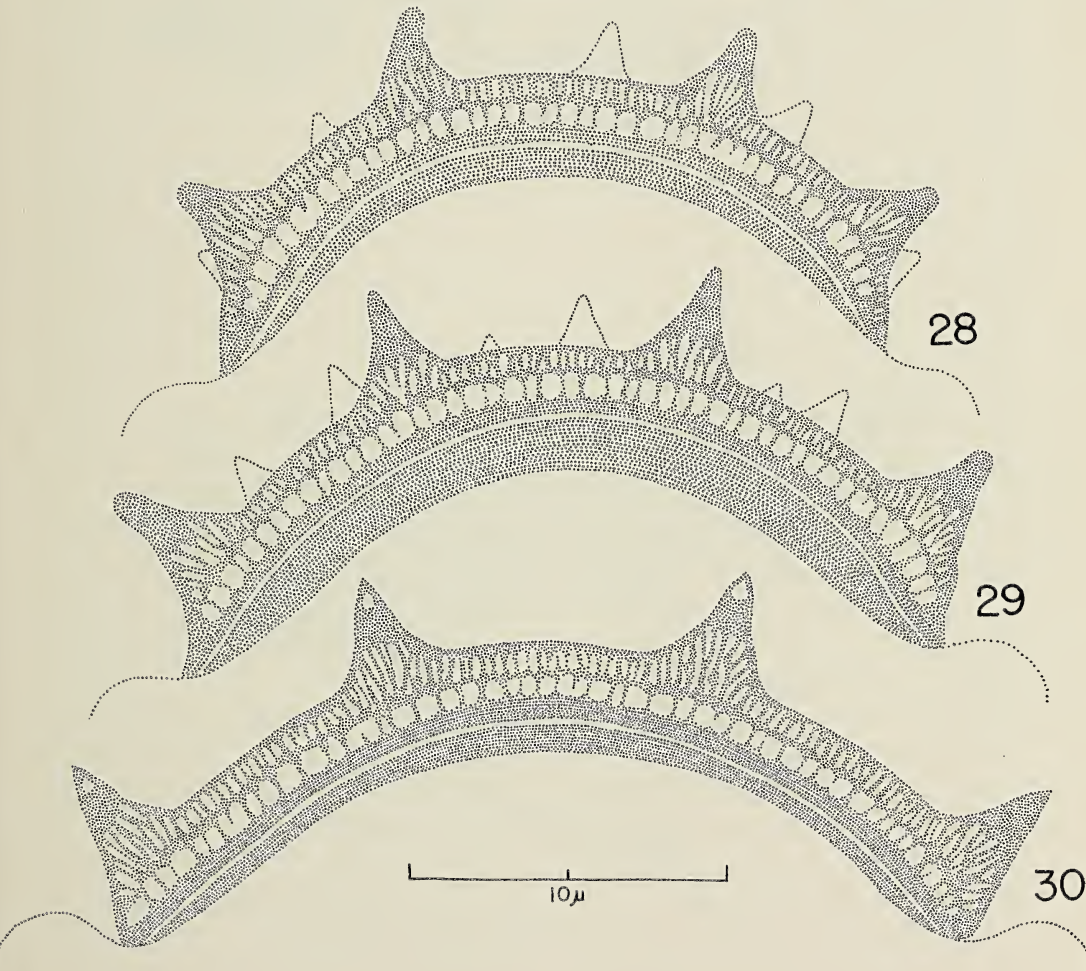


FIGS. 25-27. *Fitchia rapensis*. Fig. 25: Tip of corolla lobe, showing exterior surface; sclerenchymatous cells in black. Fig. 26: Corolla, showing venation. Fig. 27: Stamen tip, showing inner surface. Figs. 25, 27, $\times 65$. Fig. 26, $\times 8$.

match those of the typical *F. cuneata* (Carlquist, 1957:32). In *F. cordata* (Fig. 28) the spines are even more markedly blunt. Pollen grains of *F. cordata* (range, 39–51 μ ; average, 42 μ) are the smallest in the genus. The pollen grains of *F. cuneata* ssp. *tabaaensis* (range, 45–51 μ ; average, 48 μ) closely match those of ssp. *cuneata* in size. The slightly smaller size of grains in the latter may be caused by the fact that flowers of *F. cuneata* ssp. *cuneata* from which grains were taken were not quite mature. Pollen grains of *F. rapensis* (Fig. 30) average 60 μ in diameter, and have a range from 51 to 66 μ . They are thus slightly larger than those of *F.*

mangarevensis, although the difference is not significant. The spines of pollen grains of *F. rapensis* have an inverted-funnelform shape, like those of *F. mangarevensis*, but appear to be more sharply pointed. In addition, lacunae in spine tips were observed for the first time in the genus in *F. rapensis*. This feature, however, is not unexpected in *Fitchia*, since other Heliantheae have lacunae in spine tips (Carlquist, 1957:33).

SPECIES CHARACTERISTICS: In the monograph three species groups were recognized: (1) *F. speciosa*; (2) *F. nutans*, *F. tabitensis*, and *F. cuneata*; and (3) *F. mangarevensis* and



FIGS. 28–30. Optical sections of equator of pollen grains, showing a third of each grain. Germ pores indicated at left and right in each. Fig. 28, *F. cordata*. Fig. 29, *F. cuneata* ssp. *tabaaensis*. Fig. 30, *F. rapensis*.



31



32

FIGS. 31-32. Type specimens of *Fitchia*. Fig. 31, *F. cordata*. Fig. 32, *F. cuneata* ssp. *tahaaensis*.

F. rapensis. The new taxa clearly belong to the second group. The present study also emphasizes the distinctness of the third group and the close relationship between the two species it contains.

Fitchia cuneata ssp. *tahaaensis* agrees with typical *F. cuneata* in most respects. Those by which it differs include: presence of sclerified tyloses in wood (not yet observed in wood of typical *F. cuneata*); leaves with wider and longer laminae; secretory cavities present in leaf mesophyll; involucre bracts thicker; sclerified trichomes on corolla-lobe tips longer and fewer; anther tips longer. These differences are relatively minor. Close identity of the two subspecies is revealed by such critical features as general leaf shape, pith structure, bract anatomy, corolla vascularization, awn shape and anatomy, and pollen size and ornamentation. The two taxa are therefore best regarded as subspecifically different. This situation is precisely what one would expect on account of the closeness of Tahaa to Raiatea, sister-islands (within a common fringing reef).

The nearest island to the sister-islands of Raiatea is Bora Bora. One might expect, therefore, a similarity between *F. cuneata* and *F. cordata*. These two do appear similar in their small heads, relative lack of sclerenchyma in involucre bracts, venation and size of corollas, lack of secretory cavities in leaves (excepting ssp. *tahaaensis*) and blunt shape of spines on pollen grains. They are dissimilar in that *F. cordata* possesses secretory canals and thin-walled nonlignified cells in the pith, has cordate leaves, and some sclerenchyma along veins of leaves. These characteristics are reminiscent of *F. nutans*. From *F. nutans*, however, *F. cordata* differs by such respects as those in which it resembles *F. cuneata*. Features of *F. cordata* which do not match those of any species in the *F. nutans*-*F. cuneata*-*F. tahitensis* group include the presence of nonlignified cells in pith, the small leaf size and cordate shape combined with relatively long petiole length, the presence of both long multiseriate sclerified trichomes and sclerified epidermal cells on corolla-lobe tips, long stamen tips, small pollen size, and blunt spines on pollen grains. These characteristics, combined with the distinction furnished by its geographical isolation on Bora Bora, mark *F. cordata* as worthy of recognition as a new species.

PHYLOGENETIC CONSIDERATIONS: The new taxa described here, although they contribute no anomalous features to the genus, do enlarge our picture of it and permit more detailed observations in this regard. The monograph of the genus provided some notions on the relationships of *Fitchia*. These ideas do not seem to require alteration. The new taxa do enhance the diversity of the Society Islands *Fitchias*. Indeed, Papy (1955) notes that the Society Islands form a center of diversity for *Fitchia*, and that the variability of *Fitchia* on Tahiti is suggestive of this. The latter phenomenon remains a problem worthy of study when more material from Tahiti becomes available.

Postulation of phylogenetic trends within each species group seems inadvisable, both because of the limited quantity of material known and the fact that the species seem to be variations on a basic theme rather than stages along a phylogenetic pathway. However, some interpretations of relationship among the species groups may be offered here.

The larger size—in all parts of the plant—of *F. speciosa*, as compared with the remaining species, seems specialized. The larger pollen size suggests the possibility of a greater chromosome number, and the morphology of the awn base seems clearly a specialized feature. The fact that *F. speciosa* has such an isolated geographical position, the westernmost species of *Fitchia*, in contrast with the likelihood of an American ancestry of this helianthoid (e.g., Brown, 1935; Papy, 1955), reinforces this supposition. The extremely large seeds of *F. speciosa* seem less adapted to long-distance dispersal than the smaller seeds of the Society Islands species. The most likely interpretation, seemingly, is that seed size, and the peculiar adnation of achene summit to awn base in *F. speciosa* are characteristics acquired subsequent to arrival of its ancestors in Rarotonga. *Fitchia speciosa* may be regarded as a highly distinct derivative of the Society Islands stock. Although corollas of *F. speciosa* are the largest in the genus, their venation is like that of the Society Islands species, not that of *F. rapensis* and *F. mangarevensis*, which have complex corolla venation.

If pollen-grain size is an indication of chromosome number, then one would expect the Society Islands species to have the lowest num-

ber, and progressively higher chromosome numbers would be indicated for the *F. rapensis*-*F. mangarevensis* group and *F. speciosa*. If this were true, and it were a criterion of phylogeny within the genus, the complex floral venation of *F. rapensis* and *F. mangarevensis* would be a specialization. Information on comparative cytology within the genus, in any case, is highly desirable.

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Lithoglyptes hirsutus (Cirripedia: Acrothoracica), A New Burrowing Barnacle from Hawaii

JACK T. TOMLINSON¹

TWO SAMPLES of coral from Kaneohe Bay, Oahu, Hawaii, have each yielded a number of specimens of a new species of acrothoracican burrowing barnacle of the family Lithoglyptidae. Samples of *Psammocora verrilli* Vaughan collected by Stephen A. Wainwright,² and of *Porites compressa* Dana collected by Charles Stasek,³ were referred to me by William A. Newman.³ These barnacles are the first representatives of the order Acrothoracica known from Hawaii.

FAMILY LITHOGLYPTIDAE Aurivillius 1892

Lithoglyptidae *emend.* Tomlinson and Newman 1960.

Mouth cirri well developed, on a 2-jointed pedicle; 4-5 pairs of terminal cirri, but if only 4 pairs, caudal appendage present; no gut teeth or gizzard in digestive tract; with adhesive disc on mantle; lateral bar absent; burrows in coral or mollusc hard parts.

Lithoglyptes Aurivillius 1892 (*emend.*)

Four pairs of terminal cirri on a 2-jointed pedicle with oblique sutures at first joints; caudal appendage present; mouth cirrus with 2 rami of 3 to 6 articles (5 to 6 in original description).

Lithoglyptes hirsutus n. sp.

DIAGNOSIS: Female (Figs. 1-7): Mantle aperture strongly arched on both sides of an acute projecting tip which is not a movable

spine or hook; aperture length exceeds $\frac{1}{2}$ of mantle width, aperture armed with numerous teeth and long flexible hairs, especially on the outer edge of the lip area; anterior and posterior rami of mouth cirri with 5 and 3 articles, respectively; caudal appendage with 2 segments; head with acute projection opposite mouth area; burrow pointed oval in surface view. Holotype 1.2×0.67 mm; about 30 dried specimens in *Psammocora verrilli* from a depth of 3-6 ft on Sand Bar Reef and in *Porites compressa* from NE side Checker Reef, Kaneohe Bay, Oahu, Hawaii. The species is named for the presence of numerous hairs on the mantle aperture.

TYPE MATERIAL: Holotype USNM 107544. Paratype material: San Francisco State College, San Francisco, California; California Academy of Sciences, San Francisco, California; Plymouth Laboratory, England; Seto Marine Biological Laboratory, Japan; Portobello Marine Station, New Zealand.

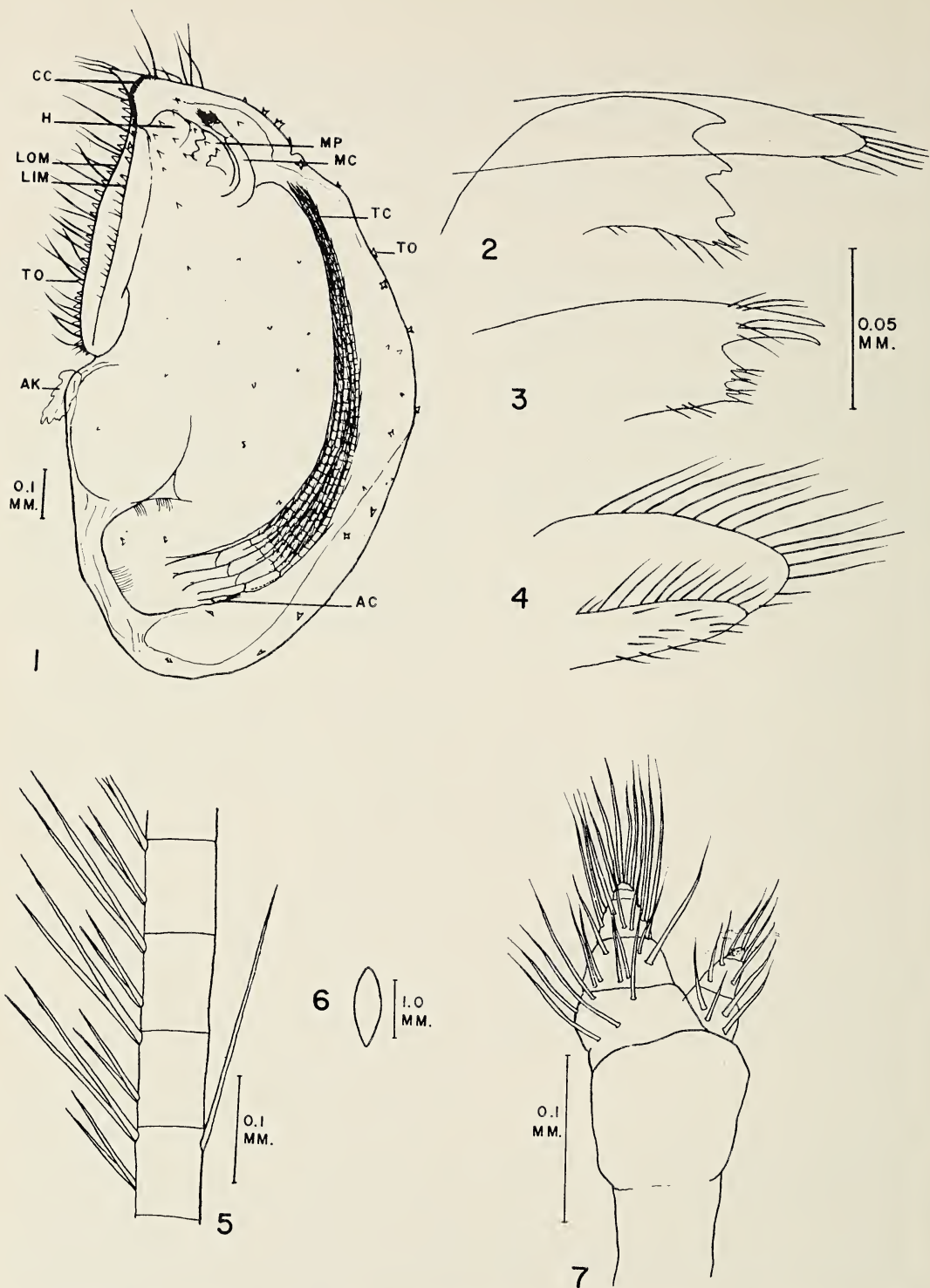
DESCRIPTION: Female: The mantles of 16 adults averaged 1.95 mm in height $\times$ 1.18 mm in width (maximum 2.1 mm and 1.6 mm), and are flattened laterally. The mantle is studded with numerous small T-shaped teeth, short spinules, and three- or four-pointed star-shaped teeth, all scattered about on the surface, but particularly near the aperture. The mantle attachment disc adheres strongly to the burrow, but is readily removed if the coral is decalcified.

The average length of the slitlike aperture of 12 specimens is 0.97 mm. Near the anterior end of the aperture two acute projections extend to a point, but are not movable or hooked. The outer edges of the thickened apertural area are heavily set with teeth and long hairs. The inner edges have fewer teeth and hairs, but have a row of comblike projections which extend into the aperture and tend to occlude it. This structure has been called the "comb-collar" by previous workers.

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FIGS. 1-7. 1, *Lithoglyptes birsutus*, n. sp., female, side view of adult removed from burrow; abbreviations: AC, anal cirrus; AK, attachment knob; CC, comb collar; H, head; LIM, lip of mantle aperture, inner margin; LOM, lip, outer margin; MC, mouth cirrus; MP, mouth parts; TC, terminal cirri; TO, tooth.

2-4, Mouth parts of *Lithoglyptes birsutus*, n. sp., female; 2, mandible with palp; 3, first maxilla; 4, second maxilla.

5-7, *Lithoglyptes birsutus*, n. sp., female; 5, middle portion of fourth (last) terminal cirrus, side view; 6, burrow in coral, surface view; 7, mouth cirrus, slightly foreshortened in comparison with some specimens.

The mouth parts (Figs. 2-4) are typical for the genus, being composed of a pair of mandibles with palps and two pairs of maxillae. Each mandible has four strong teeth, the inner one bearing short bristles. The mandibular palp exceeds the mandible in length; with long, soft bristles on the edges near the tapering point. Each first maxilla is armed with two strong teeth, numerous bristles, short teeth along the cutting edge, and has the usual apodeme. The second pair of maxillae are large and soft, and have numerous flexible bristles distributed along their edges. These close-set appendages serve as posterior limits to the mouth field.

The mouth cirri (Fig. 7) have a two-jointed pedicle upon which the two bristle-bearing rami articulate. They arise below the mouth parts but terminate above them, frequently curving outward at the tips. The anterior ramus has five segments and the posterior ramus has three segments. The segments of the rami are equipped with numerous bristles, which make the determination of the number of segments very difficult.

There are four pairs of biramous, multisegmented terminal cirri, on two-segmented pedicles. The slanted articulation between these pedicular segments is characteristic of the genus. The rami are armed with single long setae on the outer edges of every second to sixth articulation. The setae on the inner edge of the terminal cirri alternate between pairs of long setae at the articulation and pairs of shorter setae toward the middle of the segment (Fig. 5).

A pair of two-jointed uniramous caudal appendages occurs at the posterior end of the body. The total length of the caudal appendage is about $\frac{1}{2}$ the length of the pedicle of the posterior terminal cirrus.

The burrow of the female appears in the surface view as a pointed oval (Fig. 6). It is deeper than it is long. The walls are nearly perpendicular to the surface, and rounded at the bottom. The depth of the burrow appears

to be slightly more than the greatest diameter of the animal in dried specimens. It is assumed that the living animal closes the burrow opening with the hardened, hairy apertural area of the mantle.

MALE: Dwarf males resembling cyprid larvae were seen, but being dried they were much distorted, and whether or not they were truly mature stages could not be determined. Of the 11 males studied, none had the very reduced baglike shape of many acrothoracican males, nor the attenuated stalk of the male of *Lithoglyptes spinatus*. They were of a size and shape one would expect of a cyprid larva which had lost its bivalved carapace. The presence of a penis could not be ascertained.

L. hirsutus is the first member of the genus to be found in the central Pacific. Of the other species in the genus *L. indicus* Aurivillius, *L. ampulla* Aur., and *L. bicornis* Aur. are from the Java Sea and Indian Ocean, and *L. spinatus* Tomlinson and Newman is from Jamaica.

L. hirsutus can be distinguished from *L. bicornis*, *L. ampulla*, and *L. spinatus* by the absence of the apertural hooks and/or spines borne by the latter three species. This new species may be distinguished from *L. indicus*, which also lacks the hooks and spines, by the presence of the "hairs" on the mantle aperture and by its small size (2×1 mm rather than 6×4 mm).

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Toxicity of Dialyzed Extracts of Some California Anemones (Coelenterata)¹

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ABSTRACT: Anemones of the California coast, collected from November 1960 to March 1961, were compared with respect to their toxicity. Aqueous extracts of the anemones were dialyzed and assayed by intraperitoneal injection to mice, and the survival times of the injected mice were compared.

The extracts of *Anthopleura elegantissima* and *A. xanthogrammica* were by far more toxic than those of *Metridium senile*, *Corynactis californica*, *Tealia crassicornis*, *T. lofotensis*, and *T. coriacea*.

The differences in potencies of the extracts may indicate species variations in (1) toxicity, (2) efficiency of the extraction method, or (3) both.

THE AQUEOUS EXTRACTS of many coelenterates are poisonous (Dodge, 1957). The poisons are mixtures of biologically active compounds (Crescitelli and Geissman, 1962), some of them amines (Welsh and Prock, 1958), others heat-labile colloids (Martin, 1960; Mathias et al., 1960). The poison occurs in both the nematocysts and the nematocyst-free structures of the anemones (Lane, 1960; Martin, to be published). Both the chemical composition and the biologically active substances of extracts vary from one species of anemone to another (Mathias et al., 1960; Bergmann et al., 1956). The present study was designed to compare the lethality in mice of dialyzed extracts of some anemones of the California coast.

MATERIAL AND METHODS

SPECIES AND SITES OF COLLECTION: Anemones were collected at various sites on the California coast from November 1960 to March 1961: *Anthopleura elegantissima* from Bodega Bay, Tomales Bay, Monterey, and Corona del Mar; *A. xanthogrammica* from Tomales Bay and

Monterey; *Metridium senile* from Monterey; *Corynactis californica*, *Tealia lofotensis* and *T. crassicornis* from Bodega Bay, all intertidal; and *T. coriacea* off Marineland from a 30-ft depth. In addition, the intertidal Nudibranch *Diaulula sandiegensis* and the Mollusca *Crassostrea gigas* and *Mytilus californianus* were collected at Tomales Bay. *Anthopleura elegantissima* is common all along the California coast. Its extracts were used as the base of comparison with those of the other species available.

The anemones were placed in the laboratory in aerated aquaria, with sea water which was renewed twice a week. Water temperature varied between 13 and 20 C. The anemones were exposed to the light of the laboratory. They received no food supplement. Specimens which did not show normal vitality in the aquaria were discarded. After 2-4 weeks the anemones were removed from the aquaria and cleaned from adherent objects. During this manipulation they contracted firmly. Their body wall was then punctured to empty pockets of trapped water. Then the anemones were rinsed with distilled water for 10-15 sec, blotted with mild pressure, weighed in air, and their volume determined. The specimens weighed from 0.3 to 34.2 g.

EXTRACTION: The anemones were homogenized with three times their volume of distilled water at high speed in a Waring blender for

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two 1-min periods. After being centrifuged for 30 min at 1000 g the supernatant was decanted and centrifuged again. The resulting supernatant extract was turbid but did not contain cells or debris. It was either decanted or, when it was found covered with a lipid layer, removed with syringe and needle; then its pH was determined. The extract was dialyzed for 4 hr through commercial cellophane tubing against ten times its volume of 0.001 M sodium phosphate (pH 6.2) in 0.8% sodium chloride with 1% activated charcoal (Weinberger, 1936). The dialysis was repeated once with fresh solution. All operations were performed at room temperature.

Extracts of the other lower metazoa were prepared in the same manner. All extracts were assayed immediately after their preparation. The potency of extracts of each species was compared with that of an extract of *A. elegantissima* prepared on the same day.

ASSAY: The extract was given intraperitoneally to DAL-Swiss albino mice weighing 17 to 23 g. The mice were placed in cages in lots of four to eight (Russell et al., 1960), and observed for 24 hr; their survival time was recorded. The abdominal cavities of the mice were inspected post mortem and mice with intraperitoneal hemorrhage were discarded. This condition was found in animals that showed severe pain reaction immediately after the injection and died within 4 min. The discarded animals were replaced by supplementary ones to complete the series. Each extract was assayed on a series of at least four mice.

EXPERIMENTS AND RESULTS

Preliminary experiments explored the effect of varying doses of extracts of *A. elegantissima* on the survival time of the injected mice. Only the area of LD₉₉ was considered. A dose effect curve showed that with decreasing doses the survival time increased. At the dose of 20 cc of extract per kilo of mouse, both the range and the mean of the survival time were within practical limits; therefore, this dose was selected as a convenient reference.

The pH of all the extracts varied from 6.0 to 6.6.

At a dose of 20 cc of extract of *A. elegantissima* per kilo of mouse, the mean survival time of the injected mice varied from 8 to 36 min among the ten series tested. Between some of these series the difference in survival time was significant at the 2% level by the Chi-square test. The cause of these differences is unknown. The differences showed no correlation with variations in the size, sites of origin, or dates of collection of the specimens, or with the pH of the extracts. They were not relevant for the present study.

Table 1 shows that the potency of extracts may vary from one species of anemone to another. The highest potency, as estimated by the survival time of mice after intraperitoneal injection, was found for the extracts of *A. elegantissima* and *A. xanthogrammica*. Extracts of other anemones were far less potent even when their dose was tripled. With extracts of *T. lofo-*

TABLE 1
COMPARISON OF THE SURVIVAL TIME OF MICE AFTER INTRAPERITONEAL INJECTION
OF EXTRACTS OF ANEMONES

SPECIES	NO. OF BATCHES	NO. OF MICE	DOSES CC OF EXTRACT/KG OF MOUSE	SURVIVAL TIME IN MINUTES		PROPORTION OF MICE SURVIVING 24 HR
				Mean	Range	
<i>Anthopleura elegantissima</i>	10	48	20	15.7	5-47	1/48
<i>A. xanthogrammica</i>	2	10	20	9.2	6-15	0/10
<i>Metridium senile</i>	1	6	20	174.1	80-240	0/6
<i>Corynactis californica</i>	1	5	60	138.5	118-180	0/5
<i>Tealia crassicornis</i>	1	6	60	342.8	252-480	0/6
<i>T. lofotensis</i>	1	4	20		336	3/4
<i>T. lofotensis</i>	1	4	60		460-540	2/4
<i>T. coriacea</i>	1	4	20		264-640	2/4
<i>T. coriacea</i>	1	4	60		480-900	2/4

tensis and *T. coriacea* it was not possible to obtain an LD₅₀.

The extracts of the Nudibranch *Diaulula sandiegensis* and the Mollusca *Crassostrea gigas* and *Mytilus californianus*, each assayed on six mice at the dose of 60 cc extract per kilo of mouse, caused transitory depression of activity of the injected mice, but not death.

The extracts of all anemone species lost their toxicity when they were heated at 90 C for 20 min.

DISCUSSION

The storing of the anemones alive for 2 weeks or longer before preparing the extracts was intended to minimize the amount of possibly toxic products from food ingested by them. The dialysis of the extracts was aimed at minimizing their content of biologically active amines. The nature of the non-dialyzable toxins is not known. They may be proteins similar to those demonstrated by various authors in other coelenterates (Mathias et al., 1960; Farber et al., 1961).

We found information concerning the chemical components of the anemones here investigated only in the literature on *A. elegantissima* (Bergmann and Landowne, 1958). In general the lipid content of coelenterates is high, and the proportions of various lipids and soaps and their chemical nature vary from one species to another (Bergmann et al., 1956; Bergmann and Landowne, 1958). The solubility of proteins is affected by lipids, and if it is assumed that the poisons here studied are proteins, it can be speculated that the solubility of these poisons may vary from one species to another.

The data of Table 1 suggest that the toxicity of anemones may vary from species to species. This interpretation is supported by the great difference between species with respect to potency of extracts, which was observed even when the dose of the weaker extracts was tripled. But it is also possible that the efficiency of the extracting method, and hence the poison content of the extracts, may vary from species to species. This consideration applies equally to our study and to other authors' reports of species variation in toxic compounds. These causes for variation may coexist.

Lethal effects on mice were observed with extracts of the anemones but not with extracts of the Nudibranch and the two bivalves. This suggests that toxicity is not a property of all littoral lower metazoa.

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Ecological Observations on the Sea Cucumbers *Holothuria atra* and *H. leucospilota* at Rongelap Atoll, Marshall Islands

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IN a distributional study of the black sea cucumbers, *Holothuria atra* (Jäger) and *H. leucospilota* (Brandt), at Rongelap Atoll (Fig. 1) the beaches of most of the larger islets were surveyed during September 1959, March 1961, and September 1961. Estimates of abundance and size were made, and observations on temperature tolerance, predation, asexual reproduction by fission, and some other ecological aspects were considered.

These two species of sea cucumbers are frequently, although not always, found together in the intertidal area of the seaward sides of the islets at the edge of the reef-flat nearest shore. They occupy pools of water from a few centimeters to about one-half meter deep at low tide (Figs. 2, 3), or are occasionally entirely exposed. *H. atra* usually covers itself with a coating of light coral sand held in place by tube feet, although occasionally it is naked and black. The integument is thick and firm. This species lacks the Cuvierian organ and thus may be handled without the annoyance of adhesive threads. *H. leucospilota* is always naked and almost black, has a softer integument with fine protuberances giving it a prickly appearance. The intricate, microscopic calcareous deposits in the integument differ markedly in the two species: in *H. atra* (Fig. 4A) the "tables" are tall and there are no "buttons," while in *H. leucospilota* (Fig. 4B) the tables are short and squat, and there are many buttons.

H. atra also occurs in deeper water in the lagoon, where it does not coat itself with sand, and to an undetermined extent on the vast areas of reef-flat between islets. At high tide the water at the seaward shores of the islets usually covers both species to a depth of 1-1½ m, and they

are then frequently subjected to wave action from the surf whose initial force has been broken by the outer reef. A conspicuous feature of this habitat is the churning agitation and aeration of the water. *H. atra* appears to maintain its position by inhabiting depressions and holding onto the relatively smooth reef-flat by means of its tube feet. *H. leucospilota* usually anchors the posterior portion of its body underneath a stable rock or in a hole in the reef floor. In the absence of other cover it may find its way under a cluster of *H. atra* (Fig. 3). At appropriate times it extends its highly mobile and extensible anterior end outward for feeding.

Concentrations of these two species almost always occur where large slabs of beachrock are situated on the lower edge of the sandy beach slope bordering the inner edge of the reef-flat, and where, after the recession of the tide, the sea water may be observed to issue from the sand onto the reef-flat below the slabs of rock until the next tide. Below a sandy beach without slabs of rock no such prolonged runoff is evident, and the sea cucumbers usually are few or lacking. It is in the pools fed by the relatively cool water from underneath the rock slabs that *H. atra* and *H. leucospilota* thrive. Concentrations of sea cucumbers were occasionally seen in the absence of slab-rock, and rarely slab-rock was found without sea cucumbers. They occupy an ecological niche almost devoid of other macroscopic organisms; occasionally small snails occur, but frequently the sea cucumbers are alone. There is no obvious food in the sand they ingest.

CENSUSING OF SEA CUCUMBERS

The surveying procedure consisted of observing, photographing, and taking notes on the abundance of *Holothuria* while walking around

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TABLE 1
DISTRIBUTION OF *H. atra* AND *H. leucospilota* ON THE SEAWARD SHORES OF ISLETS
BY 100-M SECTION NUMBERS

(The body of the table shows section numbers in which the abundance of sea cucumbers fell within the range indicated in the column heading. Sections for each islet were numbered clockwise starting at the counterclockwise extremity (left-hand end when facing seaward) of the seaward shore.)

No	Islet Name	Date		100-m section number										Remarks	Total individuals observed or estimated			
		Sept. '59	March '61	Sept. '61	Numbers of <i>H. atra</i>					Numbers of <i>H. leucospilota</i>					<i>H. atra</i>	<i>H. leucospilota</i>		
					0-2 (1)*	3-10 (5.62)	11-100 (33.2)	101-1000 (318)	1001-3000 (1730)	0-2 (1)*	3-10 (5.62)	11-100 (33.2)	101-1000 (318)				1001-3000 (1730)	
2	Naen	15		19	1-5						1-5					0	0	
3	W. Yugui	15														0	0	
4	Pigani-yaroyaro	15		19	1-4		5	6			1-4		5		6	E. shore, many	210	2000
5	Aerik	22			1-3						1-2	3				12 <i>atra</i> on W. shore	12	40
6	E. Yugui	22				1-4					2-4	1				8 <i>atra</i> on E, 16 on W, shore	24	64
8	Lomuialal	14			1-5						1-5						0	0
9	Geien	14				1-4					1-4						32	20
13	13 Inner	12			(10,000 <i>atra</i> in lagoon, I. 13 & I. 15)												10000	0
13	13 Outer	12		17	1	2						2					60	240
18	Reef area	13		13	(700 meters north of Aniruru I. had 83,000 <i>atra</i> , 2600 <i>leuco</i> , and 4300 <i>Stichopus chloronotus</i>)												83000	2600
18	Aniruru	12		12			1-2					1-2				200 <i>atra</i> & 100 <i>leuco</i> , in N.E. channel	3000	150
19	Kabelle	10-14	12	2	7	3, 8, 9	0, 1, 4, 6	(10)		2-10		0, 1				200 <i>atra</i> & 100 <i>leuco</i> , in N.E. channel	3000	150
20	Namoen	12			2		6-9, 13	10-12, 14, 16-	1	2		1				4 <i>leuco</i> , S. side	2300	16
29	Mellu	17		18	2-5	1, 15	6-9, 13	10-12, 14, 16-19, 20, 18, 21		1-23						3 <i>atra</i> , 3 <i>leuco</i> , E channel	3500	13
31	Gogan	18						14, 16-19, 20, 18, 21			3-6	1-2, 7-8				8 <i>atra</i> , E. channel. Slab rock at 1-3 & 5.	330	32
34	Kieshi-echi	18					1-6			1-6							600	0
39	Eniaetok	8		9	2-3, 5-8	1, 12, 13, 15-23	4, 9	11, 14	10	1-9, 11-13, 15-23	10, 14	0				5 <i>atra</i> & 1 <i>leuco</i> , N. side	3600	24
53	Rongelap	5		8-	1-2, 3-5, 8-14, 16-21, 31-35, 37, 53, 67-69, 83-92	3-5, 6, 7, 15, 36, 42, 45, 55, 57, 61, 66, 71, 60, 62-	28-30, 22, 27, 37, 43, 44, 46, 80			1-24, 25, 41	46-48, 44, 45	50-52, 54, 55, 57-62, 64, 65, 73, 75,				some <i>atra</i> , lagoon side	3400	990
				11	8-14, 16-21, 31-35, 37, 53, 67-69, 83-92	36, 42, 45, 55, 57, 61, 66, 71, 60, 62-	22, 27, 37, 43, 44, 46, 80			26-40, 42-43, 53, 67-71, 83, 84, 88-	44, 45, 49, 56, 63, 66, 72, 74, 76	50-52, 54, 55, 57-62, 64, 65, 73, 75,						
54	Arbar	19			1, 2, 6-12, 27-29	3-5, 13-26				1-26	27-29						73	38
58	Tufa	20					19			19						200 <i>atra</i> , lagoon, mid-islet only, seen	20	0
60	Burok	20				1-12				1	1-12					1 <i>atra</i> , lagoon side	60	40
61	Pokoreppu	20		20	1					1							0	0
Total sections					76	65	66	23	3	160	41	36	1	1	(Total 110421 6327)			

*Arithmetic mean. Means in other columns are geometric.

Better agreement resulted from the use of geometric than from arithmetic means.

Analysis of the table shows that the islets had an estimated 1.7×10^4 *H. atra* and 3.7×10^3 *H. leucospilota*. In addition, an extensive area ($4 \times 10^4 \text{ m}^2$) of shallow (4–6 m) lagoon bottom off Island 13 and Island 15 (Fig. 1) was observed from a skiff to be populated with an estimated 10^4 30-cm black (not sand-coated) *H. atra* lying on the light sandy portions among the darker predominating, staghorn corals. The estimate for the 700 m of reef-flat north of Aniiro I., as far as a transverse ridge across the reef, was based on three traverses from 3 to 6 m wide: first, walking north along the middle of the reef; then back, one-third of the way in from the seaward edge of the reef; and finally, pacing west across the reef on a line 200 m north of Aniiro I., for a distance of 500 m lagoonward from the seaward reef edge. Extrapolations of the above observations to the entire

atoll suggest the following numbers of *H. atra* and *H. leucospilota*, respectively: for islet shores, 2.5×10^4 and 5.5×10^3 ; for inter-islet reefs, 4×10^6 and 10^5 ; and for shallow lagoon bottom areas, 5×10^5 *H. atra*, or a total for the entire atoll of 4.5×10^6 *atra* and 1.6×10^5 *leucospilota*.

OTHER SPECIES OF SEA CUCUMBERS

Species observed other than *H. atra* and *H. leucospilota* are mentioned in order of decreasing abundance. *Stichopus chloronotus*, the greenish-black prickly sea cucumber on the inter-islet reef-flat and on the sandy, shallow lagoon shore near the north channel of Kabelle I. was most common. Also on the shallow, sandy bottom, lagoonward from Kabelle I. we observed in mid-September 1961, during a period of extreme tides, a heavy concentration (about $1/\text{m}^2$) of 10 to 20-cm specimens of a light-colored *Actinopyga* sp. with small brown spots. Dead specimens were common on the lagoon shore of Kabelle I. The large brown *Actinopyga mauritiana* occupied the outer edge of the reef-flat. *Holothuria gyrifer*, a small tan-colored sea cucumber with white spots, was common under rocks on the seaward reef and especially in the channel north of Kabelle I. Occasional specimens of *Ophiodesoma spectabilis* were encountered under rocks.

SAND PASSING THROUGH HOLOTHURIA

The holothurians have been called the earthworms of the sea. The amount of sand passing through the gut of *Holothuria* is of interest because of the possibility of profound alteration of the ecology in those areas where sea cucumbers are abundant. Crozier (1918) has estimated that in 1.7 sq miles of bottom in Harrington Sound, Bermuda, 500–1000 tons of sand pass through *Stichopus moebii* annually (considering their average length to be 27 cm and the dry weight of the contained sand to be 46 g). He concluded that the primary effect of the feeding habits upon the environment is the moving of sand from one place to another.

Trefz (1958:14) timed the passage of sand through captive *H. atra* at about 12 hr for an average-sized specimen of 30 cm. Assuming an



FIG. 2. Inner edge of reef-flat, Rongelap I., section 29, showing *Holothuria* in pools. Sept. 5, 1959, 1025 hr.



FIG. 3. *H. leucospilota* (black) extending from underneath *H. atra* in a pool on the eastern shore of Rongelap I., Aug. 23, 1958, 1700 hr.

average gut content of 100 g dry weight, this would be equivalent to 1 gram in 7.2 min. Larger specimens required more time for passage of sand through the gut than did smaller specimens, according to the following relationship derived from her data for specimens of 25–38 cm (omitting two outlying observations):

$$t = 5.3 + 0.233 L$$

where t represents time in hours for passage through the gut, and L is length of sea cucumber in cm.

Yamanouti (1939:614) weighed the gut contents of 65 small (5–25 cm) *H. atra* and recorded an average of 17.1 g dry weight (range, 0.4–40.5 g). Time required for passage through the gut of captive specimens averaged 4.8 hr. Thus, 1 gram would be ingested every 16.8 min on the average.

Direct observation during low, daytime tides of undisturbed, feeding individuals of *H. atra*

30 cm long in their natural habitat at Rongelap Atoll showed egestion of sand at the rate of 1 g (dry basis) in from 5 to 10 min, agreeing with deductions from the data of Trefz on captive specimens. Assuming continuous feeding, at Rongelap Atoll the estimated 5×10^6 *H. atra* and *H. leucospilota* probably ingest and egest about 2.4×10^8 kg of sand yearly.

It has been pointed out by Crozier (1918) for *Stichopus moebii*, by Yamanouti (1939) for *H. atra* and other species, and by Trefz (1958) for *H. atra*, that there is virtually no grinding action or reduction in size of sand particles upon passing through the gut. Trefz has demonstrated that even such minute and delicate calcareous structures as the integumental "anchors and plates" of the sea cucumber, *Ophiodesoma spectabilis*, do not undergo perceptible dissolution in the gut of *H. atra*, but that they appear the same after egestion as before ingestion, thereby negating the idea of chemical dissolution in the gut.

In some of the scoured depressions on the seaward reef where very little sand is present, *H. atra* serves an additional function by retaining within and around itself much of the sand required in its feeding that might otherwise be washed away.

SIZE OF SPECIMENS

The length of undisturbed *H. atra* in the open ranged from about 2 to 60 cm, with estimated weights of 10 to 2000 g. We have not observed smaller ones. Frequent estimates of length during the censusing led to the opinion that the geometric mean length of *H. atra* on the islet shores is about 17 cm and of the more slender *H. leucospilota* about 25 cm. In contrast to the elongate shape of the larger specimens, the smaller specimens of *H. atra* were short and thick; in fact, the smallest (2 cm) were as thick as they were long. At the northeastern reef of Kabelle I. on September 14, 1961, 407 specimens of *H. atra* in a single pool were individually measured or estimated for length and diameter in inches, while still undisturbed, and were then placed in a container of water for volume measurement in cm^3 by displacement. The temperature of the pool ranged from about 35 to 39 C during the 5 hr re-

TABLE 2

LENGTH-FREQUENCIES OF 407 *H. atra* MEASURED
IN A POOL ON THE NORTHEASTERN SHORE OF
KABELLE ISLAND, SEPT. 14, 1961

LENGTH INCHES	NUMBER	LENGTH INCHES	NUMBER
2	5	6	98
3	8	7	29
4	78	8	14
5	159	9	8
		10	2

quired for measuring. Both the high temperature and the slight, unavoidable disturbance of adjacent individuals when picking up specimens for volume measurement resulted in a small amount of contraction. After handling, the specimens were deposited in another part of the pool. Table 2 gives the length-frequencies. These measurements show a single major peak at about 5 inches (12.7 cm), and fail to affirm the presence of other expected frequency groups.

Figure 5 is a histogram showing the volume-frequency. As with length-frequency there is a single peak (at about 60 cm³).

From lines fitted by inspection to the scatter diagram of Figure 6 the relationship of volume (V) to length (L) in the size range 5–15 cm was estimated to be:

$$V = 5.4 L^{0.94}$$

The rather abrupt increase in slope beyond 15 cm is emphasized by the visually fitted line:

$$V = 0.019 L^{3.0}$$

A few additional measurements of specimens longer than 25 cm suggest that this slope of 3.0 continues throughout the upper size-range.

TEMPERATURE TOLERANCE

Consideration of their habitat, exposed to the sun in shallow pools at low tide, would suggest a high temperature tolerance for *H. atra*. On

partly cloudy days after at least 2 hr of continuous sunshine, the temperatures of 69 pools containing *H. atra* ranged from 31.1 to 39.4 C, with mean and standard deviation of 36.19 and 2.14 C. The temperatures, determined with clinical centigrade thermometers, of eight black sea cucumbers were consistently higher than simultaneous temperatures in the sand-coated sea cucumbers alongside them (by an average of 0.25 C, standard deviation 0.16 C). After more prolonged exposure to sunlight this differential would be expected to increase. Shaded thermometers on the bottoms of the pools gave readings lower than within the sand-coated sea cucumbers, while thermometers in direct sunlight on the pool bottoms approximated those within the black sea cucumbers. Extreme differences between pool- and specimen-temperatures at any one place and time barely exceeded 1 C. Some degree of reflective insulation from the radiation of the sun is imparted to *H. atra* by the coating of light-colored sand with which it habitually covers its body, enabling it to retain a slightly lower body temperature than it does when not sand-coated, or than does the naked, black *H. leucospilota* when out in the open.

The warmest pool in which a *H. leucospilota* was found was 38.4 C, but the animal was not feeding. The usual habitat of *H. leucospilota* is cooler than that of *H. atra* because of its habit of seeking the shade and protection of rocks. Water coming in over the reef at high tide has a temperature of about 29 C. When this cool water saturates the beach it remains cool if overlain by strata of slab rock, but is warmed by the sun if the sand is exposed. *H. atra* occurred in pools of higher temperature, 39.4 C. The upper limit was not determined. Crozier (1915: 281) gives the maximum temperature of the habitat of *H. surinamensis* as 31.8 C and states that muscle coagulates at 42 C. This is only about 3 C above the highest pool temperatures in which *H. atra* has been encountered. *H. atra* is unusually tolerant of heat, and is almost the only macroscopic organism living in these warm pools at low tide on the warmest days.

FIG. 4. Photomicrographs showing calcareous deposits in the integument. A, Tables of *H. atra*. B, Tables and buttons of *H. leucospilota*.



PHOTOTROPISM

H. atra, and to an even greater extent, *H. leucospilota* are negatively phototropic since both protect themselves from strong light, *H. atra* by its sand coating, and *H. leucospilota* by seeking shelter. They usually react to quick changes in light intensity, as by withdrawal of tentacles when covered by a shadow during feeding. *H. leucospilota* reacts to a shadow by suddenly contracting under the protection of the rock where its posterior end is anchored, thus frequently requiring a quick grasp and a firm pull in order to collect this species.

PREDATION

Besides reflective insulation the sand coating of *H. atra* affords concealment. This function, however, would seem to be subordinate to that of insulation, because of the small amount of predation to which *H. atra* is apparently subjected, unless, of course, the converse obtains, that the small amount of predation may be due to the concealing effect of the sand coating. A damaged sea cucumber has been observed only once. This specimen, presumably pecked by a bird, occurred in an area where curlews had been active. In no case has an animal been observed actually preying upon *H. atra*. Crozier (1915:246) observed lightly colored parts of

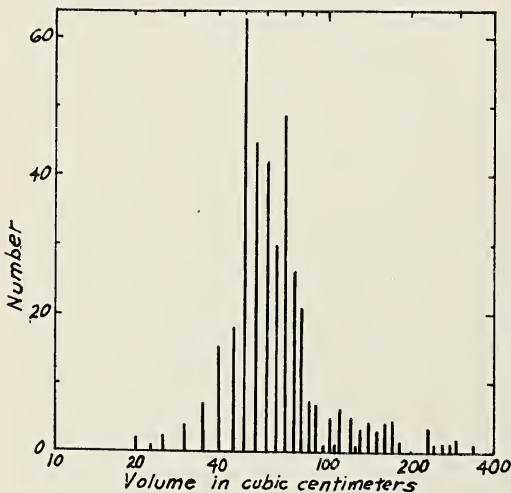


FIG. 5. Histogram showing volume-frequency of 407 *H. atra* from a pool at Kabelle I., Sept. 14, 1961.

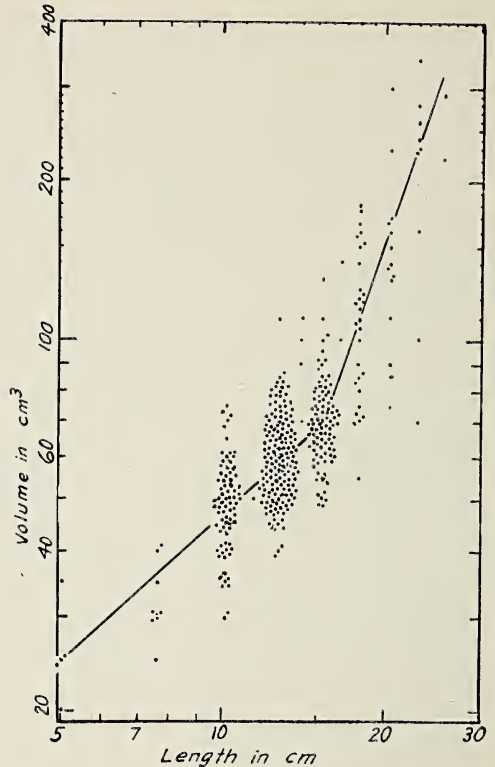


FIG. 6. Relationship of volume to length of 407 *H. atra* at Kabelle I., Sept. 14, 1961. Lines drawn by inspection.

H. surinamensis which he suspected of being regenerated following either autotomy or injury by enemies such as fishes or crabs, but states that there is no evidence that *Holothuria* has enemies of this kind. Frizzell and Exline (1955: 29) ascribe predation on intertidal sea cucumbers to sea gulls, and note the general concurrence among authors that predation is slight, but propose that the apparent protective mechanisms of holothurians suggest predation to be more common than is supposed.

TRANSVERSE FISSION

Fission has been reported in holothurians by Crozier (1915:291), who found regeneration of either end of the body in about 10% of the *H. surinamensis* encountered. Frizzell and Exline (1955:15 and 27) state that a few forms including *Holothuria parvula* (Selenka), *Cucumaria lactea*, and *C. planici* (Brandt) sometimes

reproduce by transverse fission, and that *Holothuria difficilis* Semper of the tropical Pacific commonly does so.

In September 1959 in a warm pool of about 37 C on the southwest shore of Burok I. two short specimens of *H. atra* were encountered lying end to end. The integument of the two adjacent terminal end portions was devoid of sand because of the absence of tube feet. The specimens were saved, and later examination revealed a calcareous oral ring in only one, indicating that the two individuals resulted from transverse fission. Another specimen in an adjacent pool was photographed in an advanced stage of constriction; but without disturbance by even so slight a stimulus as a shadow it voluntarily relaxed the constriction and resumed normal shape within a period of about 5 min.

During the September 1961 census, enough fissioning (Fig. 7) and fissioned specimens were

encountered to verify that fission, or asexual reproduction, does commonly occur in *Holothuria atra*.

The importance of fissioning as a means of reproduction is emphasized in Figure 6 by the relative thickness of the small specimens and the consequent reduced slope (0.9) of their logarithmic relationship of volume to length as compared to the usual cubic relationship (slope of 3) for the larger specimens.

If it may be assumed that sexual reproduction would be seasonal in nature, while fissioning would occur at all seasons, then the lack of apparent age classes or frequency modes in the volume-frequency histogram of Figure 5 is also consistent with the concept of reproduction by fissioning.

SUMMARY

1. The preferred habitat for *H. atra* and *H. leucospilota* on the seaward reef-flat is described and is linked with the presence of slabs or shelves of rock at the junction of the sandy beach with the reef-flat. On hot days runoff water from such areas is of relatively low temperature (because of the insulating effect of the slabs of rock).

2. Estimates of numbers of these two sea cucumbers are based upon notes and photographs made while traversing the peripheries of the larger islets and some reef and lagoon areas, resulting in an estimated total of about 5×10^6 *H. atra* and 2×10^5 *H. leucospilota*.

3. The passage of sand through the gut of *H. atra* is at the rate of 1 g (dry weight) in from 5 to 10 min, resulting in an estimate for the atoll of about 2×10^8 kg of sand ingested and egested yearly. The primary ecological role of the sea cucumbers in this feeding action is to move the sand from one place to another.

4. Length of *H. atra* observed ranged from 2 to 60 cm. Measurements of 407 specimens in one pool showed that for specimens up to 15 cm in length, volume increased slowly with length, while for those from 15 to 25 cm, volume increased almost as the cube of length. This is construed as evidence of reproduction by fissioning.

5. *H. atra* appeared healthy and feeding in small pools with temperatures up to 38.9 C.

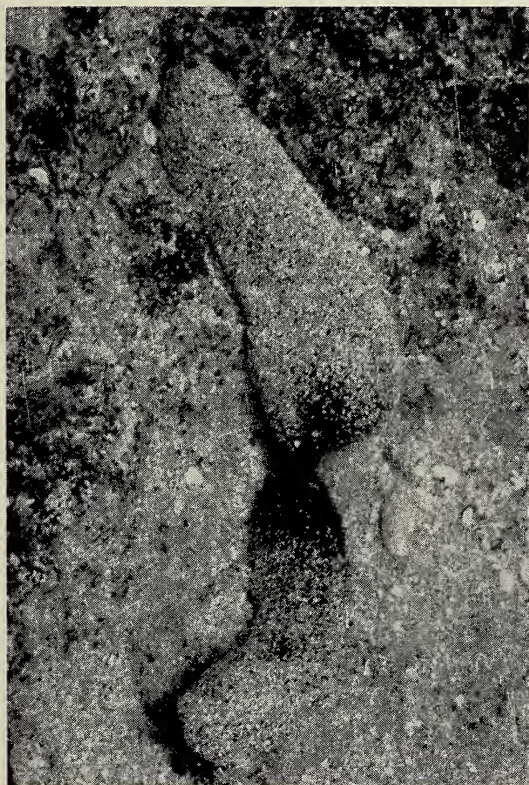


FIG. 7. *H. atra*, about 23 cm long, undergoing transverse fission in a pool 10-cm deep. Mellu I., seaward side near west end, Sept. 18, 1961, 1520 hr.

The internal temperature is slightly lower in the sand-coated than in the naked black specimens because of the reflection of light and heat by the coating of sand characteristic of this species.

6. Evidence of predation upon *H. atra* or *H. leucospilota* is practically lacking.

7. Transverse fission in *H. atra* has been observed in various stages of progress, and is considered to be an important means of reproduction.

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Field Identification of Five Species of Californian Beach Hoppers (Crustacea: Amphipoda)

DARL E. BOWERS¹

WHILE STUDYING the correlations between the distribution of five species of beach hoppers of the genus *Orchestoidea* and the physical and biotic factors of their sandy beach habitat, it became necessary to identify with certainty the animals collected from the many beaches sampled up and down the Californian coast. Since it was desirable tentatively to name the hoppers captured in the field, I made an effort to find characters which were easily observed on the beach and would allow such identification. As a result of my examination of many thousands of animals from over a hundred collecting localities, I evolved a recognition of the five species mainly on the basis of pigmentation patterns, elements of which are relatively consistent in spite of the many variations to be found in the total pigmentation.

The species under consideration are the two large hoppers, *Orchestoidea californiana* (Brandt) 1851, and *O. corniculata* Stout 1913; the two somewhat smaller species *O. columbiana* Bousfield 1958, and *O. pugettensis* (Dana) 1853; and the small species, *O. benedicti* Shoemaker 1930.

Laboratory identification of these has been made possible by E. L. Bousfield (1957, and particularly 1959), to whom I am indebted for his help with some of the key characters. In these papers Bousfield has described a new species from southern California, *O. minor*, similar to *O. columbiana*, but with a few subtle anatomical differences. These will require statistical analysis in order to show more clearly the affinities of the two species. This newly described form will not be considered here since I have been mainly concerned with the beaches of central and northern California.

The pigmentation patterns may be relied on for identification of both sexes for almost all

sizes of animals, with the following cautions: (1) The largest individuals of *californiana* almost invariably have lost the dorsal pigmentation, but color and form of the second antennae, as described below, will usually make this no problem; (2) the largest individuals of *corniculata* may have lost the dorsal pigmentation, but again, color and form of the antennae will usually suffice; (3) the smallest individuals of all species (under 4 mm in body length) may be so lightly pigmented as to make identification difficult or to require magnification and lighting available only in the laboratory; (4) animals living on white or very light-colored sands usually are only faintly marked, in which case combinations of other characters may have to be used.

Some general beach characteristics and hopper habits may also be of use in identification but are not dependable alone. *O. californiana* is typically found on long exposed beaches composed of fine sand, with few if any rocks present, beaches that are wide from the foreshore to back shore with dunes into which the hoppers may retreat during high spring tides and for breeding, beaches which usually have a quite flat foreshore, which is correlated both with exposure to wave action and with fine sand particles. *O. corniculata*, on the other hand, is typically found on shorter, more protected beaches composed of coarser sand, possibly with rocks or boulders present, beaches which may be narrow from foreshore to back shore with cliffs or piles of boulders preventing retreat during high spring tides (breeding animals are commonly found mixed with the rest of the population), beaches which may have a fairly steep foreshore, which is correlated both with protection from wave action and with coarser sand particles. These two animals are not often found together, but occasionally on a *californiana*-dominated beach, as at Carmel, California,

¹ Mills College, Oakland, California. Manuscript received January 30, 1962.

corniculata hoppers may occur at the ends of the beach where conditions are not optimal for *californiana*. I have never found *californiana* on *corniculata*-dominated beaches.

For *columbiana* and *pugettensis* I have not gathered enough data to make very meaningful statements here. They often occur together on coarse sand beaches, some of which are quite long, onto which relatively little seaweed is cast as food for the hoppers. *O. benedicti* is commonly found with *californiana*, and otherwise lives on beaches of the finest, silty sand.

It is not always easy to find mature individuals in the daylight on a beach and much sample digging is often required to locate a "bed" of hoppers. Small individuals are readily found but are not so readily captured. The distribution of hoppers on a beach is not of a random nature, but is dictated by the location of seaweed, the main food of these omnivores, on the shore, and by the tidal cycles, which they tend to follow up and down the beach. Since these animals feed mostly at night on the freshest drift present and many remain under this drift at dawn, the most productive searching is usually done under the seaweeds brought ashore by a high tide of the

previous night. Large individuals, however, may move farther up the beach; and in *californiana*, at least, the mature males and some females in the breeding season (probably February to October) with eggs or young in their brood pouches will be found scattered in fairly high and dry zones that may not have been reached by the surf for some days.

The location of the burrows of these large animals requires careful observation in the early daylight hours. In digging the burrow, or cleaning out an old one, large *californiana* kick sand out onto the surface in two opposite elongated rays. If this sand is of a different color because of a higher moisture content or because it was obtained from different-colored material below, it may be quite noticeable. However, during the day, drying action of the wind and sun may reduce the color difference between the burrow sand and the surface sand, and the winds level the elongated heaps, making them increasingly difficult to see. The burrows may be open shafts up to 12 inches in depth, with a plug of sand in the mouth of the burrow.

O. corniculata make burrow mounds much more like those of a pocket gopher. The sand is

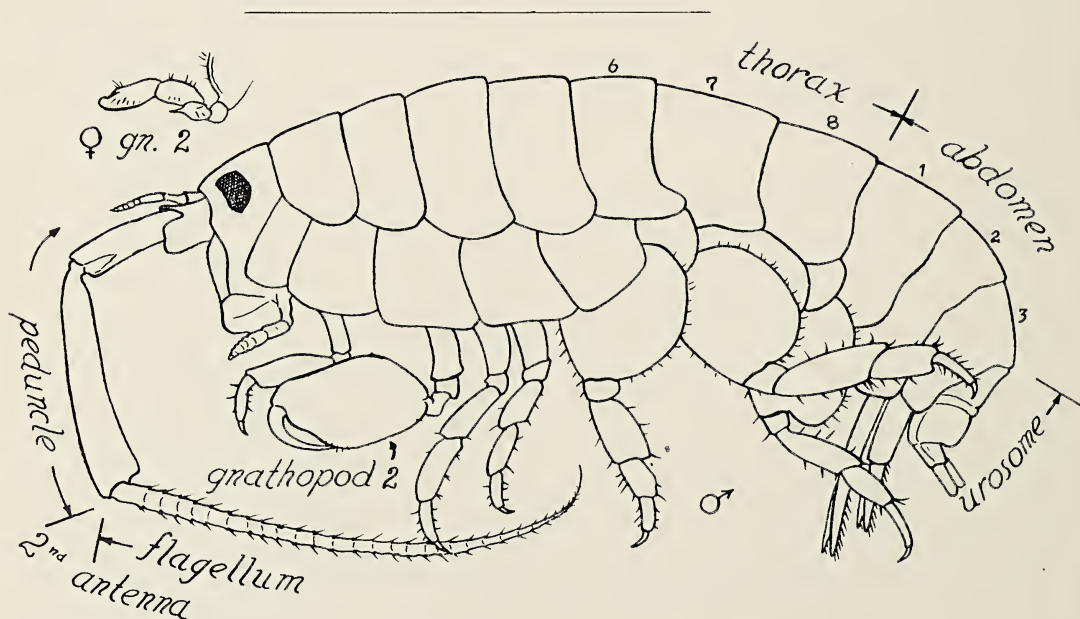


FIG. 1. Sketch of *O. californiana* to show features mentioned in the text.

pushed up less vigorously than by *californiana* and thus simply falls all around the burrow mouth in a rounded heap. Large individuals are usually found with smaller animals in mid- to high-tide zones rather than higher up on drier parts of the beach, as in *californiana*. The burrows are commonly open just around the hopper and are usually less than 6 inches deep, but I have found these hoppers more than 2 ft down.

The three smaller hopper species dig less than the large hoppers and thus do not make very obvious surface markings. They are more often found associated with washed-up debris.

I have found no sexual dimorphism with respect to pigmentation pattern, but the sex of these animals is easily distinguished by the structure of the 2nd gnathopods (the 2nd pair of large ventral appendages) except as noted below (see Fig. 1). In females the sixth segment is a fleshy paddle-shaped structure. In young genetic males the same form is present, but it becomes modelled through a series of molts into a larger subchelate "hand" with a curved dactyl closing against an eminence of the "palm." As far as I know, males can be distinguished from females only when the change in the gnathopods begins to be apparent. In *californiana* and *corniculata* this occurs when the animals reach about 9.0 and 13.0 mm in body length, respectively (measured from the anterior of the head through the chord of the straightened but still somewhat curved body to the back edge of the 3rd abdominal segment). Sexually active females possess oostegites under the thoracic region. These are thin plates with a fringe of hairs, which overlap to form a marsupium in which eggs and young are carried. However, some large females lack these hairs, their presence apparently being dependent on the breeding cycle rather than on size. The 2nd antennae of females of all species are shorter and less robust than those of males, and are less colorful.

In midday, as the waves of a rising tide moisten a beach, it is common to see small animals moving around in the just-wet area, feeding on fresh bits of seaweed, washed up sand crabs, or seemingly just wandering. Probably all species do this, but in my experience this movement has occurred mostly with *columbiana*, less fre-



FIG. 2. Left 2nd antenna of *O. corniculata* male. Compare this with appendage in Figure 1.

quently with *californiana*. Under such conditions, an observer lying face down on the sand can use pigmentation patterns to distinguish the animals without even touching them.

The most obvious character that distinguishes large male *californiana* from male *corniculata* is the form and color of the second antennae. In *californiana* the flagellum of the antenna is relatively thin, longer than the combined length of the segments of the peduncle, and gradually tapers to the tip, which reaches back beyond the middle of the body when folded from the peduncle base. The color of the peduncle is usually rosy-red. The peduncle segments are longer but not as massive as those of *corniculata*. In *corniculata* the flagellum of the antenna is thicker than in *californiana*, is shorter than the combined length of the peduncle segments, and tapers rapidly to the tip, which does not reach the middle of the body when folded (see Fig. 2). The color is usually salmon-pink, but sometimes, on a darker substrate, may be tinged with blue or brown. Newly molted individuals of both species may be white.

The antennae of *columbiana* are *californiana*-like, but in large animals are bluish-white rather than red. The antennae of *pugettensis* are *cor-*

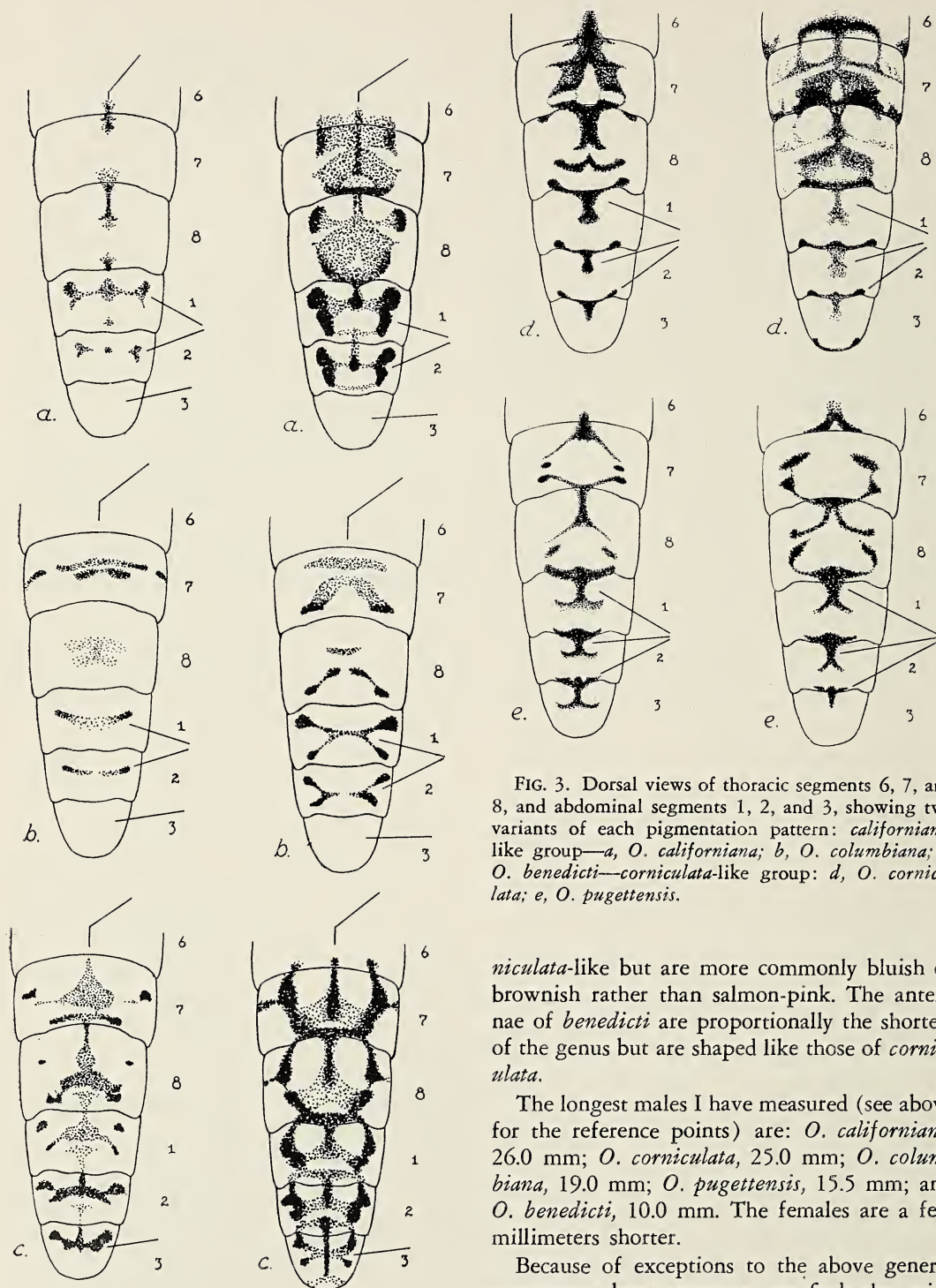


FIG. 3. Dorsal views of thoracic segments 6, 7, and 8, and abdominal segments 1, 2, and 3, showing two variants of each pigmentation pattern: *californiana*-like group—*a*, *O. californiana*; *b*, *O. columbiana*; *c*, *O. benedicti*—*corniculata*-like group: *d*, *O. corniculata*; *e*, *O. pugettensis*.

niculata-like but are more commonly bluish or brownish rather than salmon-pink. The antennae of *benedicti* are proportionally the shortest of the genus but are shaped like those of *corniculata*.

The longest males I have measured (see above for the reference points) are: *O. californiana*, 26.0 mm; *O. corniculata*, 25.0 mm; *O. columbiana*, 19.0 mm; *O. pugettensis*, 15.5 mm; and *O. benedicti*, 10.0 mm. The females are a few millimeters shorter.

Because of exceptions to the above general statements about antennae, one finds that with subadult individuals, females, and indeed even mature males from some beaches, other obvious

traits are needed for field identification. Generally, the overall pigmentation tone of these hoppers tends to match the color of the sandy substrate; but even on light sands where pigmentation is reduced, there are a few key spots that usually show up. I will be concerned mainly with the dorsum of the first three abdominal segments, which appear in a top view as the last three body segments ahead of the urosome, and the 7th and 8th thoracic segments.

A study of the sketches in Figure 3 will show that there are two main groups of pigmentation patterns. The broad "butterfly" spots of the 1st and 2nd abdominal segments of the "*californiana*-like" group are found with modifications in *O. californiana*, *O. columbiana*, and *O. benedicti*. The T-shaped spots of the 1st, 2nd, and 3rd abdominal segments of the "*corniculata*-like" group are seen in *O. corniculata* and *O. pugettensis*.

The californiana-like group. In *californiana* and *benedicti* there is a sagittal line showing in most variants of this pattern. Note the absence of pigment from the 3rd abdominal segment on *californiana*, but the presence of pigment in *benedicti*. In *columbiana* the midline marking is missing and the "butterfly" design is more nearly a flattened X, again with no pigment in abdominal segment 3. The characteristic markings of abdominal segments 1 and 2 are sufficient to separate *californiana* from *columbiana*. *Benedicti*, besides being small, is more heavily pigmented with discontinuous spots, which thus give the impression of a checkerboard design along the whole body.

The corniculata-like group. The two species in this grouping, *corniculata* and *pugettensis*, are the most difficult to separate, although they are easily distinguished from all the others. The most obvious dorsal pattern differences seem to be in the last two thoracic segments in which *pugettensis* has more delicate markings, but I have detected no easily recognizable differences here. A more consistent and reliable set of marks may be found at the lower margins of the lateral body wall in the last three thoracic segments of *pugettensis* (see Fig. 4). The third of these is missing in *corniculata*, which thus shows only two spots which are usually more diffuse and less intensely pigmented than in *pugettensis*.

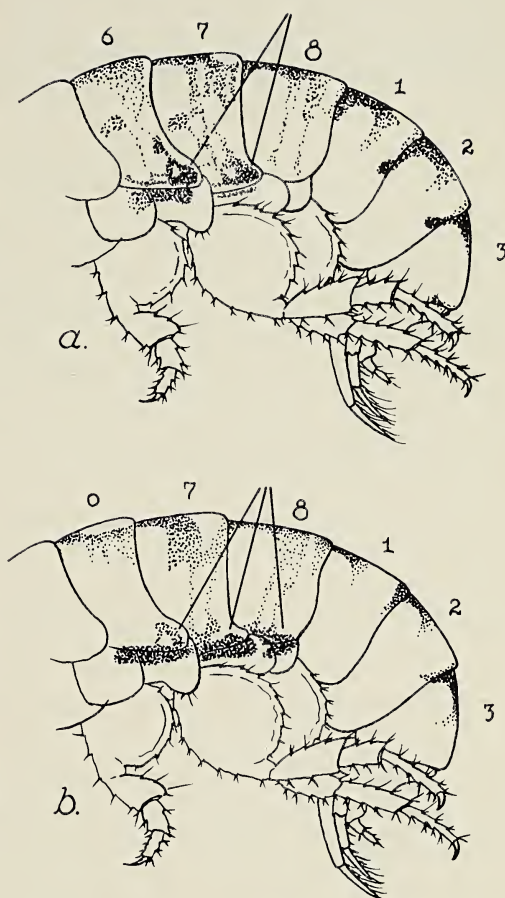


FIG. 4. Side views to show key characters of thoracic segments 6, 7, and 8. a, *O. corniculata*; b, *O. pugettensis*.

(These spots do not serve to set off these two species from the other three, however, for these others may have such markings as well.) These two hoppers are found on the same beach occasionally, and in such cases it may be necessary to rely on the key characters presented by Bousfield in the papers cited. However, these pigmentation patterns, antennae colors, and other more subtle clues allow one acquainted with the animals to make fairly reliable preliminary determinations.

Whatever "hedging" the reader may detect in this presentation is due to the wide range of variability to be found in these animals and to the fact that exceptions keep cropping up as

study continues. However, it is hoped that this discussion will make it easier to identify these animals in the field. I am grateful for financial support for this study which came in part from

the American Academy of Arts and Sciences, and in part from the Mills College Faculty Research Fund. My thanks are here expressed to Dr. Joel Hedgpeth for helpful suggestions.

FIELD KEY TO SPECIES OF *Orchestoidea*

- | | |
|---|---------------------|
| 1. Mature animals..... | 2 |
| 1. Immature animals and others not distinguished by first part of key..... | 5 |
| 2. Second antennae when folded reaching back to or beyond middle of body; flagellum longer than peduncle..... | 3 |
| 2. Second antennae when folded not reaching back to middle of body; flagellum shorter than peduncle..... | 4 |
| 3. Color of 2nd antennae rosy-red..... | <i>californiana</i> |
| 3. Color of 2nd antennae bluish-white..... | <i>columbiana</i> |
| 4. Color of 2nd antennae usually salmon-pink..... | <i>corniculata</i> |
| 4. Color of 2nd antennae not so..... | 5 |
| 5. Dorsal pigmentation pattern containing "butterfly" designs..... | 6 |
| 5. Dorsal pigmentation pattern containing T-shaped designs (Lower limb of T may be faint or missing)..... | 8 |
| 6. Mid-dorsal line absent, "butterfly" spots flattened X's..... | <i>columbiana</i> |
| 6. Mid-dorsal line present..... | 7 |
| 7. No markings on 3rd abdominal segment; sides of body relatively free of pigmentation marks..... | <i>californiana</i> |
| 7. Markings on 3rd abdominal segment; sides of body blotched with checkerboard pattern..... | <i>benedicti</i> |
| 8. Two diffuse spots on sides of body..... | <i>corniculata</i> |
| 8. Three discrete spots on sides of body..... | <i>pugettensis</i> |

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A Simple Device for Making Successive Photomicrographic Records of Large Groups of Developing Organisms¹

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IN OUR analysis of the effect of ionizing radiation upon the cleavage of sea urchin zygotes we found it necessary to take successive photomicrographs of a large number of eggs, in different samples, which had been exposed to graded doses of ionizing radiation (Hsiao and Daniel, 1960). In order to estimate the rate of cleavage of the irradiated samples of fertilized eggs it is highly desirable to follow the cleavage of each egg in every sample and make photomicrographic records for later analysis. In other words, we need to take time-lapse pictures of the developing eggs subjected to different amounts of radiation so as to calculate the rate of cleavage and correlate it with dosage. After some preliminary trials we have put together, using commonly available materials, a simple device capable of taking photomicrographs repeatedly from the same field in a series of samples of irradiated eggs at specified time intervals. By lining up, according to time, prints made from each field, each egg can be identified and its cleavage followed from the first to the last frame in the series, and its rate of cleavage can be calculated. It occurs to us that investigators who have occasion to record developmental and other recurrent phenomena may find this simple device useful. A brief description of its method of construction and manipulation is reported in this paper.

PRINCIPLES OF CONSTRUCTION

The simplest way to obtain a sequential record of a number of fertilized eggs after their exposure to irradiation or other treatment would

be to place the eggs on the stage of the photomicrographic instrument and take cinematographic or time-lapse pictures. This requires one set of instruments for each sample exposed to one specific dose. The cost of equipment and the limitation of laboratory space would rule out all sample series of reasonable size. However, if the samples are immobilized and the photomicrographic camera is brought over an exactly predetermined point in each sample to take time-lapse photomicrographs during the course of cleavage, it would be possible to make photographic records of a number of samples with one instrument. This can be done by: (1) Immobilizing samples of eggs contained in uniform-sized culture vessels, such as a culture cell on a 1- × 3-inch micro slide, in a straight line on a stage supported by a steady stand independent of the photomicrographic camera, so that when the microscope moves no motion is transferred to the samples. (2) Using a photomicrographic camera carriage made to move back and forth along a straight track placed parallel to the line of the immobilized sample cultures and adjusted to bring the microscope objective across the middle of the cultures. (3) Employing a series of uniform spacers (such as 1-inch rectangular bars for use with the 1- × 3-inch micro slide containing samples of egg cultures), whose width equals the distance between the centers of the culture vessels of two neighboring samples, to stop the photomicrographic camera carriage on the track each time the objective of the microscope reaches the center of a sample on the immovable stage. In this way a single photomicrographic camera can be used to photograph the eggs in the exact center of each sample culture vessel, and a series of the time-lapse photomicrographs is obtained for later analysis.

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² Department of Zoology, University of Hawaii. Manuscript received February 6, 1962.

MATERIAL USED AND METHOD OF CONSTRUCTION

The device built on the above principles consists of two independent parts: (A) a steady stand for supporting the cultures to be photographed, and (B) a movable carriage on which a microscope and its camera and substage lamp are mounted so that the microscope and its accessories can travel from culture to culture without disturbing the stand or the organisms on it. The materials used for the construction of this device are limited to the few simple items listed below:

- 7-ft length of 2×2 -inch wood
- piece of $28 \times 8 \times 1$ -inch plywood
- 12-ft length of $\frac{1}{2}$ -inch wide $\frac{1}{8}$ -inch thick angle aluminum
- $20 \times 8 \times \frac{1}{8}$ -inch sheet of aluminum
- 1 dozen No. 8, 1-inch wood screws
- 8 self-tapping sheet metal screws, size $3/32$ - $1/4$ -inch
- 3 aluminum sheaves, $5/8$ -inch in diameter
- 11 machine screws with nuts, size $3/32$ - $1/4$ -inch
- 6-ft length of 3-sided 1-inch-square extruded aluminum channel
- piece of $5\frac{1}{2} \times 28 \times \frac{1}{4}$ -inch plate glass

All these are easily obtainable from local hardware stores.

A. The stand. This independent part of the instrument is made of a rectangular wooden base, two aluminum trapezoidal end supports, and a rectangular glass toppiece or stage. The construction of these three parts is summarized below. (1) From the 2×2 -inch lumber, two 11- and two 31-inch lengths are cut. These four pieces are joined at right angles by means of either end-lap joint or pinned tenon-and-tusk joint into a rectangular base measuring 31×11 inches on the outside. (2) From the $\frac{1}{8}$ -inch-thick sheet of aluminum two 8×8 -inch pieces are cut and each is shaped into a near trapezoid (it will be referred to as trapezoid in this paper for simplicity), as shown in Figure 1A, by cutting off a triangular piece whose two sides adjacent to the right angle are 2 and 6 inches long (area ABC in Fig. 1A). After rounding the corners, two $5/32$ -inch holes

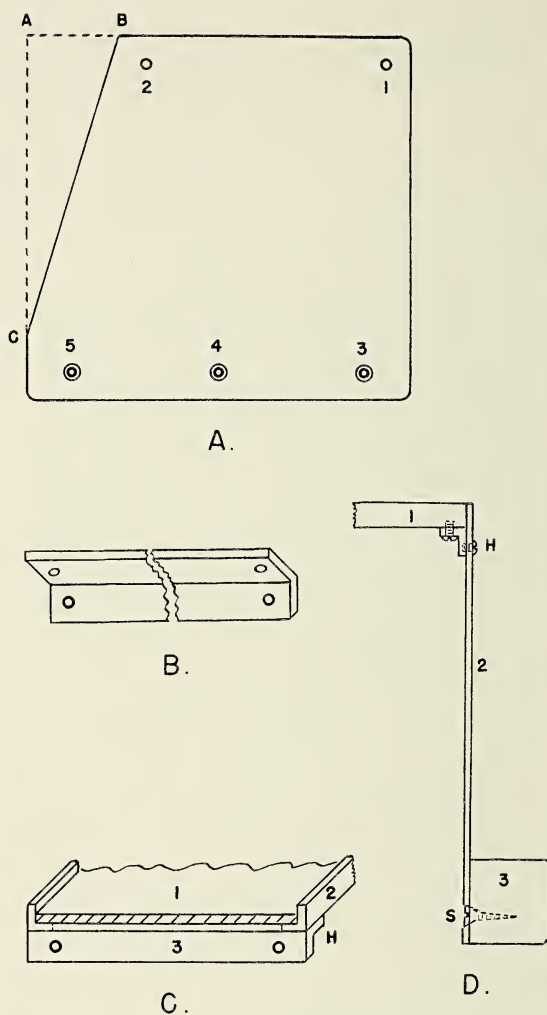


FIG. 1. Parts of the stand. A, Aluminum end support used as left end of stand. 1, 2, $5/32$ -inch holes; 1 being 1 inch from vertical edge and 2 5 inches from 1; 3, 4, 5, are three beveled holes 3 inches apart, 3 being 1 inch from vertical edge, and all $\frac{1}{2}$ inch from the bottom. B, Diagram of angle aluminum end frame for plate-glass toppiece or stage. Two upper holes $5/32$ inches, two lower ones $1/8$ inch. C, End portion of plate-glass toppiece or stage showing plate glass 1, mounted between two $28\frac{1}{2}$ -inch strips of angle aluminum, 2, which are attached on end piece, 3. The two $1/8$ -inch holes, H, are for mounting the toppiece or stage on the trapezoid end support. D, Sectional view of right end of stand, showing method of mounting trapezoidal end supports. 2, on wooden base, 3; and toppiece or stage, 1, on the trapezoid, 2. S, No. 8 wood screw; H, sheet metal self-tapping screw.

5 inches apart are drilled $\frac{1}{2}$ inch from the top and $\frac{1}{2}$ inch from the vertical edge of one of the trapezoids. Three $\frac{3}{16}$ -inch holes spaced 3 inches apart are next drilled $\frac{1}{2}$ inch from the bottom and 1 inch from the vertical edge. The holes on the second trapezoidal end support are similarly drilled but are done from the opposite surface so that this piece of aluminum forms a mirror image of the first one. (3) The rectangular glass toppiece or stage is made from a $5\frac{1}{2} \times 28$ -inch strip of $\frac{1}{4}$ -inch plate glass and a rectangular frame made of $\frac{1}{2}$ -inch wide angle aluminum. Two $5\frac{3}{4}$ -inch sections are cut from the aluminum stock and four holes drilled in each piece. Along one side of the aluminum angle two $\frac{5}{32}$ -inch holes are drilled each $\frac{3}{8}$ inch from the end, along the other side, two $\frac{1}{8}$ -inch holes, each $\frac{1}{2}$ inch from the end, are also drilled, as shown in Figure 1B. Two $28\frac{1}{2}$ -inch lengths of aluminum are cut from the same stock and two $\frac{1}{8}$ -inch holes are drilled on each piece, each hole being $\frac{3}{8}$ inch from the end. The 28-inch long plate glass is placed lengthwise between the inner surfaces of the long aluminum angle strips whose ends are then placed across the two short ($5\frac{3}{4}$ inches) end pieces in such a way that the outer surfaces of the four angle strips are in contact and the pre-drilled $\frac{1}{8}$ -inch holes on the long strips match the $\frac{5}{32}$ -inch holes on the short ones, as shown in Figure 1C, leaving the $\frac{1}{8}$ -inch holes of the short strips exposed at the ends of the frame. Four $\frac{3}{32}$ - $\frac{1}{4}$ -inch self-tapping sheet metal screws are driven through the $\frac{5}{32}$ -inch holes in the short end aluminum section tapping into the $\frac{1}{8}$ -inch holes in the long sections to hold the aluminum frame and glass together. It will be noticed that all the $\frac{5}{32}$ -inch holes are for the passage of, and the $\frac{1}{8}$ -inch holes for the tapping by, the self-tapping sheet metal screws.

To assemble the stand the two trapezoidal end supports are used to join the glass toppiece or stage to the wooden rectangular base. After placing the wooden base on a flat bench or table top, with its long sides running from left to right in front of the operator, the right trapezoidal end support is clamped with a C-clamp on the inside of the 11-inch-long end piece of the wooden base so that the vertical edge of the trapezoid faces the front of the stand, farthest from the operator and $\frac{1}{4}$ inch

from the right distal corner of the rectangular base, the slanting edge nearest the operator, the bottom of the trapezoid flush with the bench top and the smaller openings of the three beveled holes against the inside surface of the wooden end piece. After drilling three holes into the wood, using the holes in the aluminum trapezoid as guides, three No. 8, 1-inch, wood screws are driven into the wood until their heads are flush with the aluminum (see Fig. 1D at S).

The C-clamp is released. Similarly the left trapezoidal end support is screwed on the inside of the left end piece of the wooden base. The aluminum framed glass toppiece or stage is fastened to the trapezoidal end supports by apposing the two $\frac{1}{8}$ -inch holes on each end angle aluminum piece (*H* in Fig. 1C) to the two $\frac{5}{32}$ -inch holes near the top of each trapezoid and a round-head self-tapping sheet metal screw driven from the outside through the trapezoidal end support, tapping into the angle aluminum as shown at *H* in Figure 1D. When properly assembled this stand is very steady and can support a large number of culture slides or vessels on the plate glass.

B. *The carriage.* This part of the instrument consists of a platform with track, a cart for carrying the microscope and its accessories, and a number of spacers of uniform size. (1) The platform is made from a piece of $1 \times 28 \times 8$ -inch plywood and two strips of angle aluminum. Each piece of aluminum is cut 28 inches long and two $\frac{5}{32}$ -inch holes drilled through the apex of the angle, $\frac{1}{2}$ inch from each end, and beveled. One piece of the drilled aluminum is placed along the edge of the plywood board with the apex pointing upward and a No. 8, 1-inch, wood screw driven through each hole into the wood. The second piece of angle aluminum is placed parallel to the first, but with its apex $5\frac{7}{8}$ inches from that of the first, and fastened on the wood in a similar way. These two pieces of angle aluminum form the track on which the microscope-carrying cart moves. (2) The microscope-carrying cart is constructed from a piece of the $\frac{1}{8}$ -inch sheet aluminum, $5 \times 6\frac{1}{4}$ inches in size, with three pieces of angle aluminum and three $\frac{5}{8}$ -inch aluminum sheaves attached to its under surface. Six $\frac{5}{32}$ -inch holes, as indicated by No. 1-6 in

Figure 2A, are drilled through the sheet aluminum which forms the floor of the cart. A $\frac{1}{4} \times \frac{3}{4}$ -inch slit is cut at A and a round $\frac{1}{4}$ -inch hole at B, as shown in the same figure. Slit A is used to adjust and fix the substage illuminator in place, and B is for the microscope set screw, the same screw which came with the microscope for fastening it to the bottom of the microscope case during shipment. Two 5-inch sections of angle aluminum are cut, and two $\frac{5}{32}$ -inch holes drilled on each limb of the right angle. Each hole is $\frac{1}{2}$ inch from the end of the aluminum section. One of these two sections is mounted on the front undersurface of the floor of the cart with two $\frac{3}{32}$ machine screws and nuts, and the other section similarly mounted on the right undersurface at right angles to the first (Fig. 2B at 4). A third piece of angle aluminum, $1\frac{1}{2}$ -inch long is cut

and a $\frac{5}{32}$ -inch hole drilled at a distance of $\frac{1}{2}$ inch from each end. It is mounted along the back border on the undersurface of the cart floor with metal screws and nuts through openings 3 and 4 (see Figs. 2A, 2B). Three aluminum sheaves (1, 2, 3 in Fig. 2B) are mounted with machine screws and nuts on the vertical limb of the angle aluminum pieces on the undersurface of the cart floor so that sheaves No. 1 and 2 are $4\frac{1}{2}$ inches apart and each $\frac{1}{4}$ inch from the end of the 5-inch section of angle aluminum. Sheave No. 3 is mounted on the center of the vertical limbs of the $1\frac{1}{2}$ -inch section of angle aluminum and at a distance $5\frac{7}{8}$ inches from a line joining sheaves No. 1 and 2. When the cart is placed on the platform the sheaves should ride smoothly but snugly on the track. (3) The spacers are six $5\frac{3}{16}$ -inch sections cut from the 1-inch extruded rectangular aluminum channel. One spacer is mounted on the right-hand end of the platform with No. 8 wood screws, after the proper holes are drilled, to serve as the starting or ending point in the side to side movement of the microscope-carrying cart.

OPERATION OF INSTRUMENT

To employ this instrument for taking photomicrographs a microscope and a substage illuminator are mounted on the microscope-carrying cart. In our laboratory an old E. Leitz Wetzler microscope with its mirror removed is fastened on the cart floor by its set screw driven through opening B into the horse-shoe shaped base, and a Kohler illuminator through slit A. The light is centered and adjusted by standard procedures (Gray, 1958). The stand is placed on the laboratory table with its length parallel with the edge of the table and the slanting edges of the aluminum end supports near the operator. The platform is placed inside the stand so that a $\frac{1}{4}$ -inch clearing is produced on all four sides between the platform and the base of the stand. The microscope with its cart and illuminator is carefully put in place by sliding the microscope stage immediately under the plate-glass toppiece of the stand from back forward across the stand until the sheaves are over the track. The cart is lowered onto the track and pushed toward the right until it is

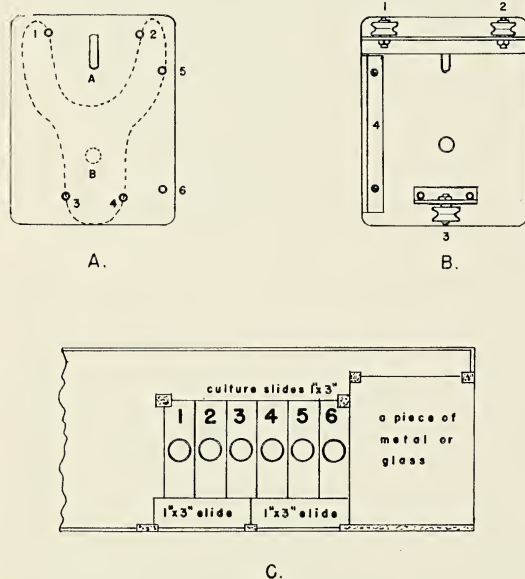


FIG. 2. Diagrams showing microscope carrying cart floor and top view of stand in use. A, Top surface of cart floor, showing openings 1 to 6 for attaching angle aluminum on undersurface; A, slit for adjusting and fixing illuminator; B, opening for microscope base set screw. Broken line indicates outline of the base of the microscope. B, Undersurface of cart floor. 1-3, sheaves; 4, 5-inch angle aluminum for buffering against spacer. C, Right portion of plate-glass toppiece of stand showing culture slides, 1-6 in place. Stippled areas represent masking tape. Other slides and glass (or metal) are positioning guides.

stopped by the fixed spacer at the end. A culture slide containing the sample is placed on the plate glass with its length perpendicular to the long axis of the glass top piece and directly under the low power objective of the microscope. In our experiments a glass or aluminum ring $\frac{3}{4}$ -inch I. D. and $\frac{5}{32}$ -inch high is mounted in the center of a 1×3 -inch micro slide with epoxy cement to serve as a culture cell. When the culture slide has been centered, a piece of metal or glass is placed snugly against its right side and fixed on the plate glass with masking tape to serve as a slide end-stop. To facilitate lining up the other culture slides on the left side of this extreme right one the 1-inch wide space between the 28-inch-long aluminum frame on the side nearest the operator and the culture slide is filled with another 1×3 -inch slide at right angles to the end-stop (see Fig. 2C). Other culture slides are then easily placed in a straight line on the left of the original one as shown in Figure 2C by pushing them toward the right lower corner against the slide end-stop. After all the culture slides are placed in a straight line from right to left, the microscope-carrying cart is moved toward the left by drawing it along the track and the 1-inch-wide aluminum spacers are placed between the cart and the end piece on the platform, the number of spacers used being equal to the number of culture slides. As both the spacers and the culture slides are 1-inch wide the slide on the extreme left will be centered directly under the microscope. The culture slides and spacers are numbered correspondingly, both starting with No. 1 on the left and ending with the highest number on the right.

A photograph of the assembled device with the photomicrographic instrument in place is shown in Figure 3.

To take photomicrographs with this device, a camera is mounted on the microscope, and the specimens in the culture cell brought into view. Usually, before the first exposure is made, the specimens are centered and arranged on each slide, using a glass needle, so that a large number of individuals can be observed in each microscope field. Once the specimens are properly arranged, no other manipulation is needed, and they will stay in place throughout the course of the experiment. After the specimens

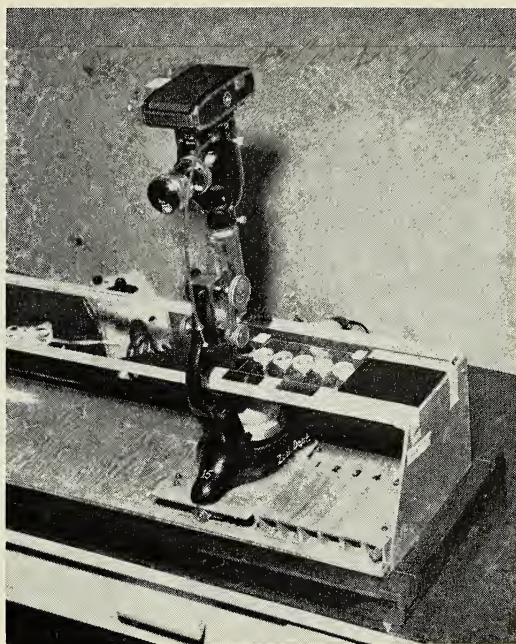


FIG. 3. Photograph of device, with camera, microscope, and illuminator in place.

are brought into sharp focus, a photograph is taken with the time of exposure and light intensity adjusted by the usual method for photomicrographic work (Shillaber, 1944). To take a photograph of the second culture, the first spacer on the left is removed, the microscope pushed 1 inch toward the right tightly against the remaining spacers, the specimens brought into sharp focus, and a second frame of the film exposed. This procedure is repeated until the microscope-carrying cart is against the stopping spacer on the extreme right of the platform, and each culture has been photographed.

To start the second series of photomicrographs, the microscope is moved to the left, all the aluminum spacers replaced on the platform, maintaining their original order, and the cart pushed tightly against them. This automatically places the microscope objective over the center of the first culture. After a predetermined time lapse, the process of photomicrography described above is repeated, taking a second photograph of each one of the cultures, covering, in each case, exactly the same field as in the first run. The exact time of day a photograph is taken is noted down, and later

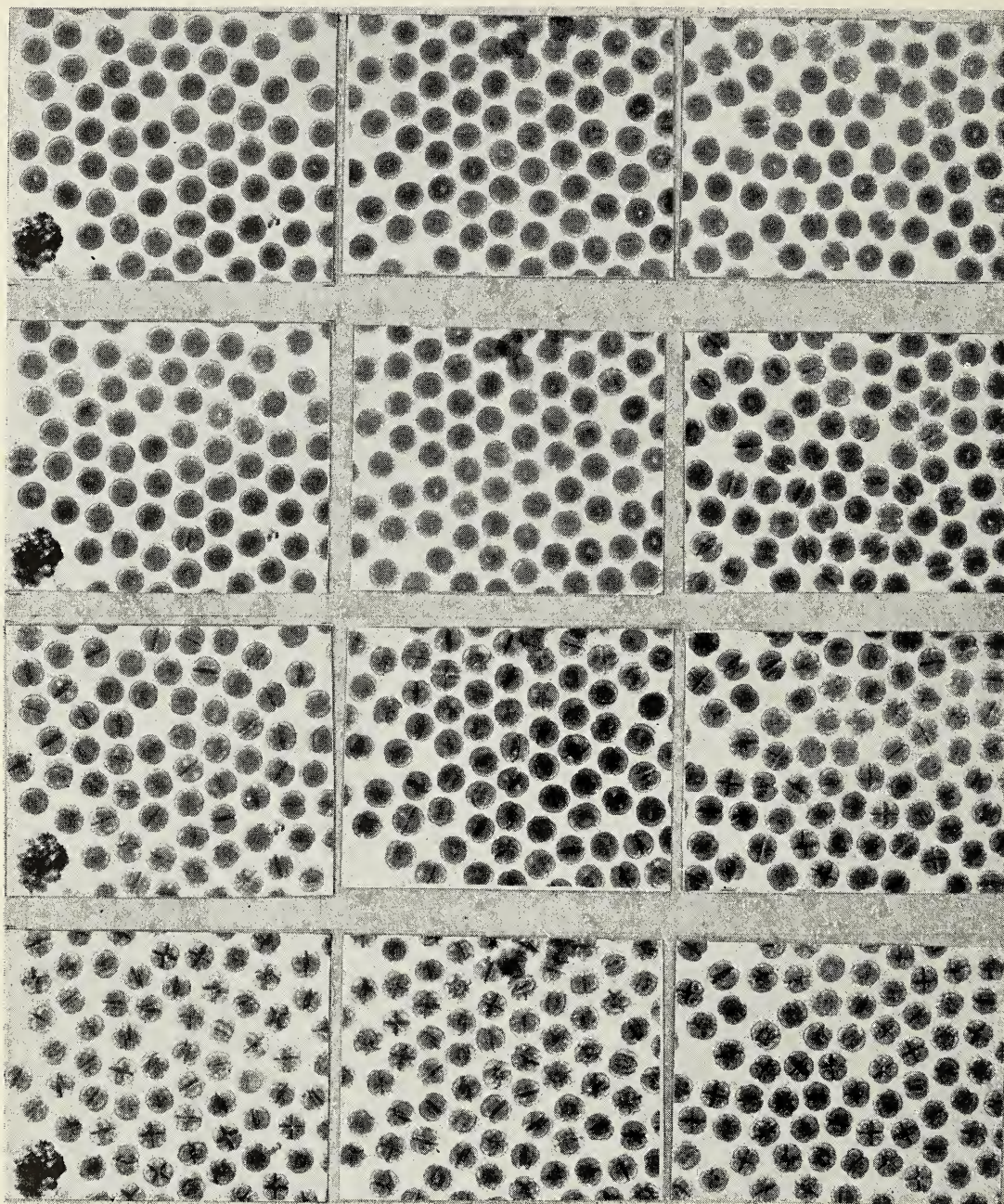


FIG. 4. Examples of time-lapse photomicrographs taken with the device. Each vertical column represents one sample culture in an X-irradiation experiment. Column 1 is the control, or Or; column 2 was subjected to 5r; and column 3 to 20r. The top horizontal row was taken at 1:25 P.M. or 85 min post-fertilization. The second horizontal row was taken at 1:30 P.M.; the third row at 2:15 P.M.; and the fourth row at 3:00 P.M. or 180 min post-fertilization.

transcribed onto the print. In one of our experiments, for instance, six cultures of eggs, each culture having been treated with a different dose of X-irradiation, were photographed successively within 3 min. In this way, a series of time-lapse photomicrographs, each bearing the time of day when it was taken, was made for each sample culture from the zygote to a desired stage, such as morula, and the resulting photographic prints analyzed and the rate of cleavage calculated. In Figure 4 selected examples of sequential photographs are reproduced to show the stability of the relative position of the eggs and their structural change during cleavage.

To identify each egg and estimate its rate of cleavage, a tracing of the first photograph of each sample is made on transparent paper. The drawing of each egg to be followed is given a number. By superimposing the tracing on the second or any subsequent time-lapse photograph of a particular sample culture, the eggs can be individually identified. The time it takes for an egg in a given sample culture subjected to a specific treatment to attain a certain developmental stage, (for instance, the attainment of the four-cell stage by a zygote after acute exposure to 20 roentgens), is determined by subtracting the time of fertilization from the time the picture was first taken which shows the desired stage of the egg. Thus, in one experiment the eggs were fertilized at 12:00 noon, the two-cell stage of egg No. 38 first appeared in the photograph taken at 1:30 P.M.; the four-cell stage at 2:15 P.M.; and the eight-cell stage at 3:15 P.M. Thus we can deduce that it took 90 min for 1st cleavage, 135 min for 2nd cleavage, and 195 min for 3rd cleavage.

DISCUSSION

1. Blum and Price (1950) described an apparatus for following photographically the cleavages of sea urchin eggs. They pointed out two advantages of the photographic method: (1) more accurate timing of the cleavages than fixing followed by counting; (2) the cleavages of each individual egg can be followed and recorded. Blum and Price used two microscopes in the inverted position, one for U-V-ray irra-

diated eggs, and the other for controls. The present device requires only one microscope.

2. In our instrument, observation is not limited to one treatment, i. e., one sample of treated animals compared with its control. In the present device, a large number of samples, each receiving a special treatment, can be compared with one or more untreated control or controls, using only one photomicrographic apparatus. A stand 28-inch long as used in our apparatus, can accommodate 20 or more samples at one time. The only limit to the number of samples is the time required for making one run of photography through the whole set of samples, and that required for making photographic print-analyses later. With this apparatus (as with Blum and Price's) the change in cleavage rate due to treatment such as X-irradiation can be recorded. For example an increase or decrease in the rate of cleavage can be observed; or initial retardation followed by recovery is made apparent. Similarly, the course of abnormal development can be followed; some of the abnormalities may disappear, others may persist. Fixing of eggs and later examination can not provide a sequential series of recorded events, especially recoveries. Furthermore, the eggs from a single female can be used in all of these samples, thus eliminating individual variations resulting from the use of batches of eggs from different females.

3. The instrument described here is one version of our device. Other modifications both in the material used and in details of construction are possible. For instance, we have also applied two coiled springs symmetrically to the microscope-carrying cart in order to pull the entire carriage tightly against the aluminum spacers. Another modification is the use of a light cooling and filtering device. A shallow transparent tray containing cold water can be placed on the plate glass between the culture samples and the light source.

ACKNOWLEDGMENT

We are indebted to Dr. Walter R. Steiger and Mr. George Yokotaki of the University of Hawaii physics department for their advice and machine-shop help.

SUMMARY

A simple device for taking time-lapse photomicrographs of a group of cultures of eggs to show the development of each individual has been described. This device is made of readily available material. It consists of two parts: (1) A piece of plate glass supported by a frame which is steady and independent of the motion of the photomicrographic apparatus. It serves to replace the stage of the microscope and to carry the eggs in cultures in a motion-free state. (2) A carriage for the photomicrographic apparatus which can be made to travel back and forth in a straight line from left to right, repeatedly bringing the microscope and its camera to a specific field in each culture for sequential photomicrography.

The device has the advantage of being simple, easy to construct and operate, and it can be used to follow photographically an individual egg during its early development from zygote to morula as well as to record the appear-

ance, disappearance, or persistence of developmental abnormalities. Other recurring phenomena can also be studied photomicrographically by this instrument.

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Revision of the Genus *Pandanus* Stickman, Part 15 Malayan Species Described by H. N. Ridley

HAROLD ST. JOHN¹

AS IN MANY OTHER GENERA Henry N. Ridley, director of the Botanic Garden, Singapore, made noteworthy contributions to the knowledge of the Malayan species of *Pandanus*. His species were validly published in local journals or in his books. He described them briefly, usually giving some details of the stem, leaves, appearance of the syncarp, length of style, and width of the exposed tip of the drupes. He cited specimens but did not adopt the type method. None of his species were illustrated. The writer has investigated Ridley's species, sought the holotypes or has chosen lectotypes in the Singapore herbarium. These specimens were kindly made available by the present director, Dr. H. M. Burkill.

Ridley's species of *Pandanus* are nearly all good, and these are to be maintained. He placed most of his species in either the section *Rykia* or in *Acrostigma*. As will be noted in the treatment that follows, additional sections are to be found among his species. The large majority of Ridley's species are treated in this article; and the few remaining ones will be illustrated and described in subsequent parts when their type specimens have been located and studied.

SECTION *Acrostigma*

Pandanus aurantiacus Ridl., Roy. Asiat. Soc., Straits Branch, Jour. 41: 49 (1904) = 1903; Fl. Malay Penin. 5: 81, 1925; Martelli, Webbia 4(2): t. 30, figs. 10-13, 1914; (sect. *Acrostigma*)

Fig. 172

DIAGNOSIS OF LECTOTYPE: "Large branching shrub with stems 3.6 m. tall, 5-7.5 cm. through"; leaves "glaucous green"; the lower bracteal leaf 1.26 m long, 4.2 cm wide, coriaceous, 1-ribbed

but 2-pleated and in section M-shaped, the blade sword-shaped, from the base gradually tapering to the approximately 20 cm long subulate apex which about 10 cm down is 1.5 mm wide, at midsection each side with 42 parallel secondary nerves, the base amplexicaul and unarmed but beginning 7-8 cm up the margins with serrations 0.6-0.9 mm long, 1-2.5 mm apart, pale; the midrib below from 21 cm up with serrations 0.3-0.5 mm long, 2-10 mm apart, subulate-tipped; at midsection the margins and midrib below with serrae 1-1.5 mm long, 1-3 mm apart; near the apex the margins and midrib below with rigid serrulations 0.4-0.6 mm long, 2-4 mm apart; pistillate inflorescence 43 cm long, 12-13 mm in diameter, trigonous, bracted, spicate, bearing in the terminal 20 cm 5 syncarps which are orange and subequal; syncarps 6-7 cm long, 5-5.5 cm in diameter, ovoid to broadly ellipsoid, bearing about 160 drupes, these 21-22 mm long, 3.5-5 mm wide, 3-4 mm thick, lower $\frac{2}{3}$ oblanceoloid, upper $\frac{1}{3}$ subulate, 4-6-angled, the body sides smooth, later with exposed fibers; pileus 10-11 mm long, of a lower half narrowly conic-pyramidal, the surface smooth, sharply angled, the angles continuing along the stout subulate style forming the upper half, arcuate proximally; stigma 3 mm long, linear, in a distal cleft running almost to the apex; endocarp centering in lower $\frac{1}{3}$, and 7-8 mm long, the walls pale, 0.3 mm thick; apical mesocarp a broad cavern 2 mm long; basal mesocarp fibrous up the sides, fleshy within.

EXPANDED DESCRIPTION: Shrub to 5 m tall; stem with the leaf scars inconspicuous; prop roots 60 cm long; leaves to 2 m long, 4-5 cm wide, above clear green, below paler and glaucous; foliage leaves little broadened at base, the margins beginning at 4 cm up with prickles 1.6-2 mm long, 2-5 mm apart, stout subulate, ascending; the midrib below beginning at 9

¹ B. P. Bishop Museum, Honolulu 17, Hawaii, U. S. A. Manuscript received July 19, 1961.

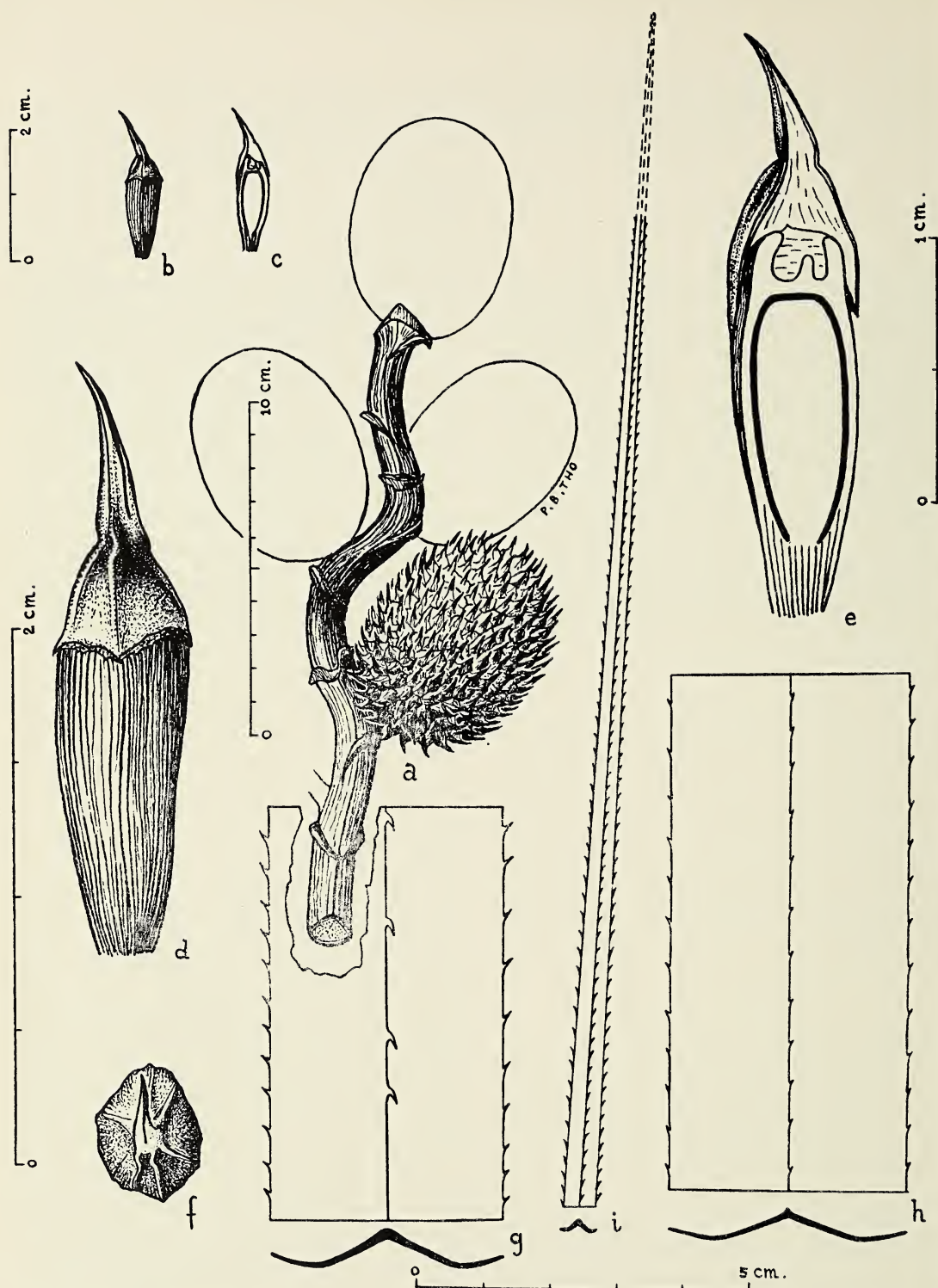


FIG. 172. *Pandanus aurantiacus* Ridl., from lectotype. *a*, Infructescence, $\times \frac{1}{2}$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, style, and stigma, apical view, $\times 4$; *g*, leaf base, lower side, $\times 1$; *h*, leaf middle, lower side, $\times 1$; *i*, leaf apex, lower side, $\times 1$.

cm with prickles 3–3.5 mm long, 8–20 mm apart, very stout subulate, strongly reflexed; pistillate scape 15–40 cm long, bearing 3–9 syncarps, these 5–7 cm long; drupes very hard until ripe when they become bright reddish orange and soft.

LECTOTYPE: Singapore, Bukit Timah [Bukit Mandai Road], 1894, *H. N. Ridley*, (SING). Specimen examined and herein designated as lectotype.

SPECIMENS EXAMINED: Singapore, Pasir Panjang, 17 Oct. 1912, *I. H. Burkill & M. R. Henderson* 6,802 (BO, SING). Malaya: Johore, Pulau Kukub, 1904, *H. N. Ridley* (paratype), (SING).

Ridley, when publishing this species, cited three collections and mentioned Sarawak, but did not designate a holotype. The most complete of his original specimens is here chosen as the lectotype.

Pandanus collinus Ridl., Mater. Fl. Malay Penin. 2: 228, 1907; Fl. Malay Penin. 5: 79, 1925; Martelli, Webbia 4(1): 10, 1913; (sect. *Acrostigma*)

Fig. 173

DIAGNOSIS OF LECTOTYPE: Shrub 1.2–2.1 m tall; stem at summit 6 mm in diameter, brownish, smooth; leaves 25–45 cm long, 8–11 mm wide, firm chartaceous, apparently pale green on both sides and flat except near the base where 2-pleated, 1-ribbed, above unarmed, at the middle with 10–11 secondary parallel veins in each half, below the tertiary cross veins barely visible, gradually narrowed in the last 10 cm to a subulate tip 15–20 mm long and 0.6–0.8 mm wide, the base amplexicaul, unarmed, blackish purple, beginning at 2 cm from the base the margins with prickles 0.7–1 mm long, 3–7 mm apart, subulate, ascending, yellowish but red-tipped; the midrib below unarmed to well beyond the middle; at mid-section the margins with subulate tipped serrulations 0.2–0.3 mm long, 1.5–3 mm apart, appressed ascending, red-tipped; near the apex the margins with serrulations 0.1–0.2 mm long, 0.3–0.5 mm apart; the midrib below with serrulations 0.2–0.3 mm long, 0.5–1.5 mm apart; pistillate inflorescence terminal, erect, bearing 1 head; peduncle 8 cm long, 3 mm in diameter,

bracted; syncarp 3 cm long, 2.5 cm in diameter, subglobose, bearing about 88 drupes, these 14–15 mm long, 4–5 mm wide, 3–4 mm thick, the body ellipsoid to obovoid, 5–6-angled, 10 mm long; pileus with the base 3.5–4 mm high, semiorbicular or slightly narrower, rather smooth, but with longitudinal ridges and lines; style 4–5 mm long, abruptly subulate, angled, sharply proximally curved, bony; stigma 3–4 mm long, elliptic-linear, brown, papillose, extending to the tip; endocarp centering in lower $\frac{1}{3}$ but extending to the base, the walls 0.1 mm thick, cartilaginous, stramineous; seed 7.5–8 mm long, lance-obovoid; upper mesocarp an oblate hemisphere, filled with white medullary membranes; basal mesocarp fibrous up the sides, fleshy within, sparse.

LECTOTYPE: Malaya, Kedah, Kedah Peak, woods, 1893, *H. N. Ridley*, (SING). Specimen examined and here designated as lectotype!

DISCUSSION: *P. collinus* belongs in the section *Acrostigma*. It was described by Ridley from three collections from Malaya. The best of these and the one labeled *P. collinus*! by Ridley is here chosen as the lectotype. Contrasting differences are given for this in our treatment of *P. alticola*.

Pandanus glaucophyllus Ridl., Roy. Asiat. Soc., Straits Branch, Jour. 41: 50, (1904) = 1903; (sect. *Acrostigma*)

Fig. 174

DIAGNOSIS OF HOLOTYPE: "Stems 3–4 m. tall, 12–25 mm. in diameter," the internodes brown to yellowish, smooth, mostly higher than the nodes; leaves 52–60 "or more" cm long, near the base about 4 cm wide, near the apex 5.7–6.5 cm wide, appearing narrowly oblong, rather flaccid and when dry chartaceous, glaucous, 1-ribbed but 2-pleated and in section low M-shaped, the secondary parallel veins conspicuous and 34 of them in each half, the apex abruptly contracted to a 6–7 cm trigonus subulate caudate prolongation which near its base is 1 mm wide, the base of the blade amplexicaul and unarmed, but beginning at 4 cm up the margins with prickles 0.5–0.8 mm long, 1–3 mm apart, slender subulate, pale, ascending or diverging and some of them doubles or triples; the midrib

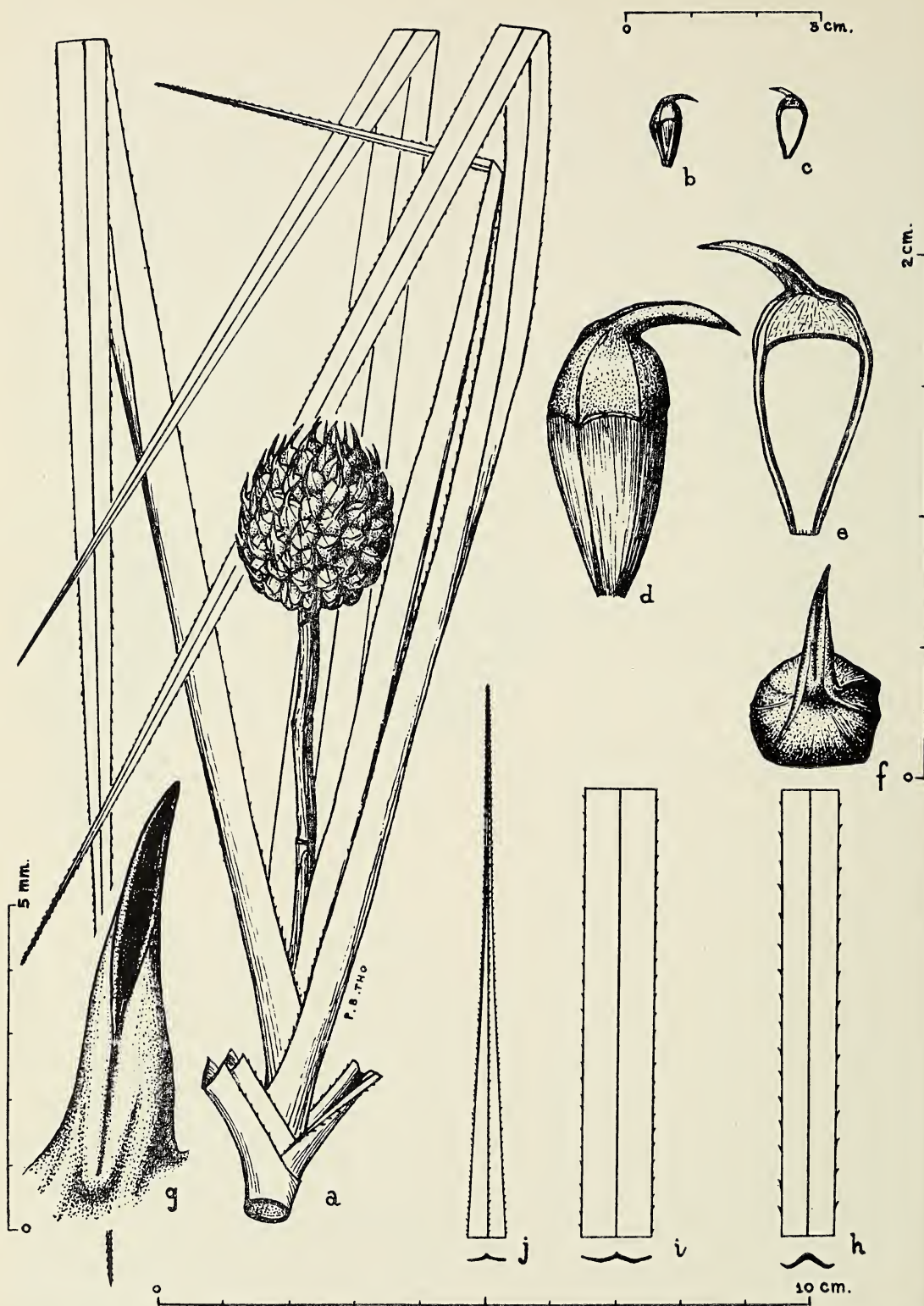


FIG. 173. *Pandanus collinus* Ridl., from lectotype. *a*, Habit and syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, style, and stigma, apical view, $\times 4$; *g*, style and stigma, distal view, $\times 10$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$.

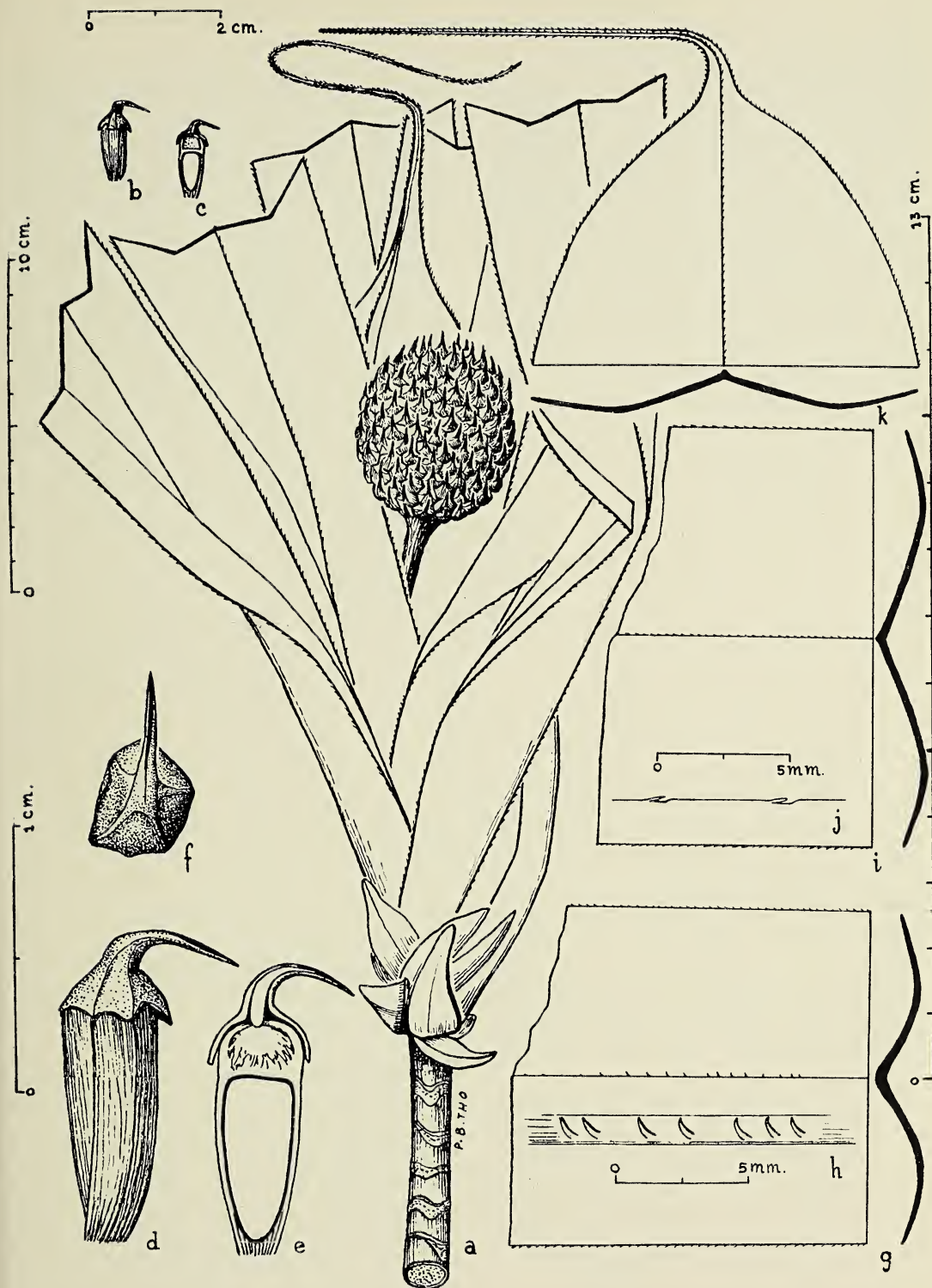


FIG. 174. *Pandanus glaucophyllus* Ridl., from holotype. *a*, Habit and syncarp, $\times \frac{1}{2}$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, style, and stigma, apical view, $\times 4$; *g*, leaf base, lower side, $\times 1$; *h*, midrib, lower side, near base, $\times 4$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf margin, near middle, $\times 4$; *k*, leaf apex, lower side, $\times 1$.

below beginning at 4–9 cm with prickles 0.8–1 mm long, 0.5–6 mm apart, slender subulate, brownish, ascending, oblique, closely appressed; at midsection the margins with prickles 0.5–0.7 mm long, 1–3 mm apart, slender subulate, ascending flat appressed and occupying recesses in the margin; the midrib below glabrous or with a few prickles like those lower down; at the bend of the apical contraction the margins with prickles 0.6–0.8 mm long, 0.6–1.5 mm apart, slender subulate, somewhat ascending or divergent; the midrib with prickles 0.6–1 mm long, 1–2 mm apart, arcuate subulate, ascending; on the caudate tip the margins and midrib below with prickles 0.3–0.7 mm long, 0.3–1.5 mm apart, stout arcuate subulate, ascending; pistillate peduncle 8 cm long, 7 mm in diameter, erect, bearing a single syncarp 5.7 cm long, 4.5 cm in diameter, broadly ellipsoid, bearing about 320 drupes, these 12–13 mm long (or 16–18 mm following the curve of the stigma), 5–6 mm wide, 3.5–4.5 mm thick, the body narrowly oblong ellipsoid, 5–6-angled, the sides smooth; pileus smooth, the base 3–3.5 mm long, conical or broadly so, bearing the terminal style 5–6.5 mm long, stout subulate, strongly curved proximally, having a distal cleft nearly its whole length in which is the stigma 3–4 mm long, linear, brown, papillose, running to the tip; endocarp pale brownish, centering in the lower $\frac{1}{3}$, its walls 0.1 mm thick; seeds 7–8 mm long, oblance-oblong; apical mesocarp a cavern 2–2.5 mm long, invaded by trichomes and hairs; basal mesocarp with fibers up the sides and the center fleshy.

HOLOTYPE: Malaya, "Perak, Thaiping Hills, in dense forest about 2500 feet altitude," above tea border, Dec. 1898, *H. N. Ridley* (SING). Holotype examined!

Pandanus parvus Ridl., Roy. Asiat. Soc., Straits Branch, Jour. 33: 71, Jan. 1900; Fl. Malay Penin. 5: 78, 1925; *P. flagellifer* Warb., in Engler's Pflanzenreich IV, 9: 80, Dec. 21, 1900; Martelli, Webbia 4(1): 14, 1913; 4(2): t. 33, f. 7, 1914; (sect. *Acrostigma*)

Figs. 175, 176

DIAGNOSIS OF HOLOTYPE: "Stem 2.92 cm. tall, 12 mm. in diameter, slender, branched

above," rooting throughout; leaves 27–37 cm long, near the tip 32–36 mm broad, near the base 16–20 mm broad, appearing ligulate, but actually tapering downwards, thin subcoriaceous, dark green above, pale and glaucous beneath, 2-pleated and in section low M-shaped but only 1-ribbed, the midrib below narrow and raised, the secondary parallel veins prominent throughout, and at midsection 18–21 on a side, the tertiary cross veins faintly visible below near the tip, making small squarish meshes, near the apex abruptly rounded contracted to a 3–6 cm caudate deltoid subulate tip 0.8 mm wide, the base amplexicaul, unarmed for 4–5 cm, then the margins with prickles 0.7–1.3 mm long, 2–7 mm apart, slender subulate, straight or slightly curved, brownish, ascending; the midrib below unarmed to near the apex; at midsection the margins with similar prickles 0.5–1 mm long, 4–12 mm apart; on the rounded apical contraction the margins with prickles 0.5–0.8 mm long, 0.5–2 mm apart, stouter subulate, slightly ascending; the midrib below with prickles 0.8–1.4 mm long, 1–7 mm apart, arcuate subulate, slightly ascending; on the caudate tip the margins and midrib below with stout prickles 0.3–0.8 mm long, 0.5–1.5 mm apart, subulate, arcuate, ascending; in the series of bracteal leaves the first several 2–4 cm long, lance-navicular, entire; pistillate inflorescence 1-headed; peduncle 5 cm long, 4–5 mm in diameter, 3-angled, few bracted; syncarp erect, 3.5 cm long, 3.3 cm in diameter, ovoid-globose, bearing about 150 drupes, these 11–12 mm long or following the curve 14–15 mm long, 3.5–5.5 mm wide, 2.5–3.5 mm thick, fusiform, the body 7–8 mm long, oblanceoloid, the surface smooth, later fibrous; pileus smooth, apparently glaucous, 9–10 mm long, the base oblong-pyramidal and with the apex oblique and proximally curved, tapering into a hornlike style which is 5–6 mm long, all (except the apical ones) sharply proximally curved, stigma 4–5 mm long, lance-linear, dark brown, papillose, extending to the tip; endocarp in lower $\frac{1}{4}$, stramineous, bony, the walls 0.3 mm thick, and the lateral walls extending upwards to bound the apical cavity; seed 5 mm long, oblanceoloid, truncate at tip; apical mesocarp a cavern filled with white medullary ascending hairs; basal mesocarp sparse, fibrous and fleshy.

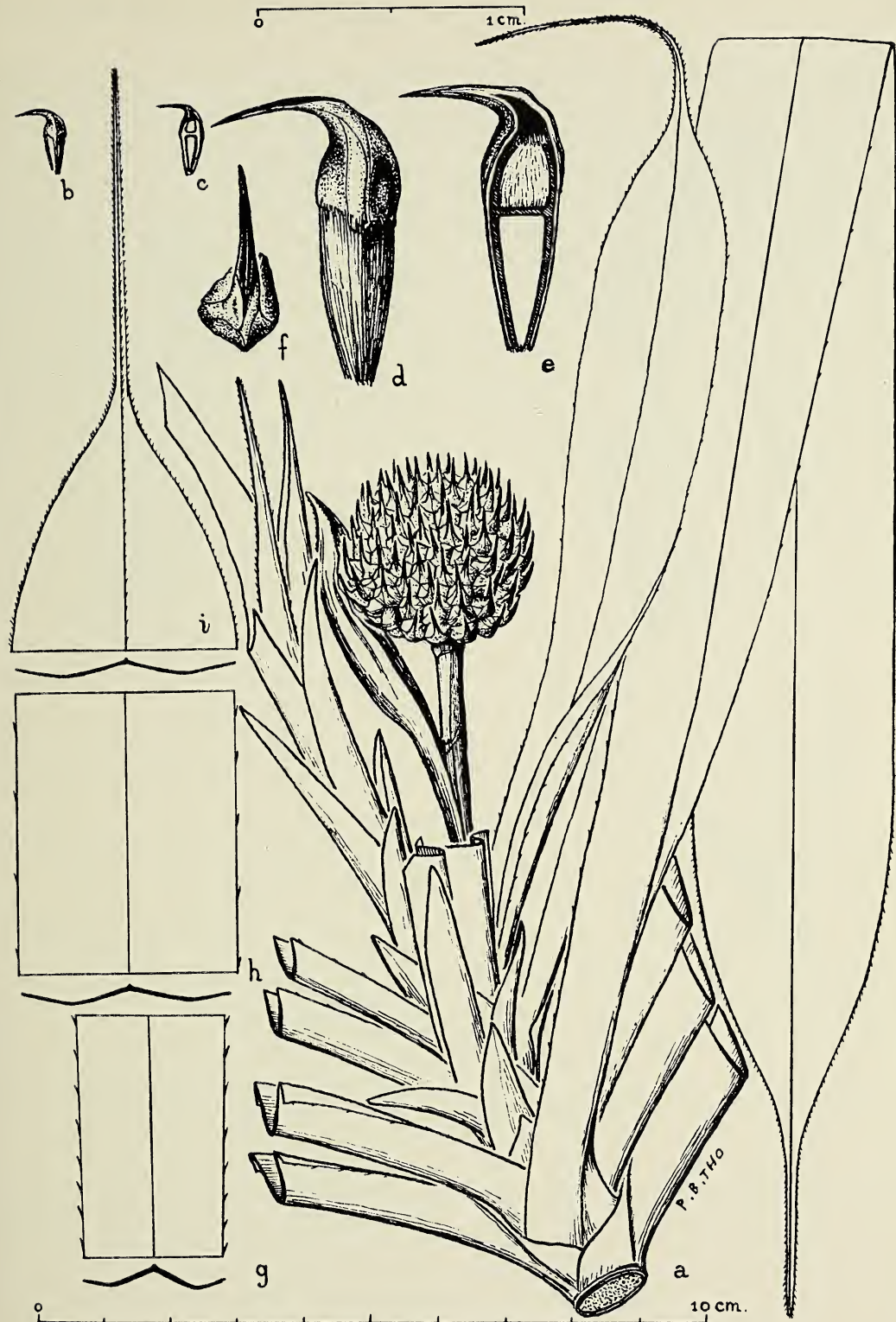


FIG. 175. *Pandanus parvus* Ridl., from holotype. *a*, Habit and syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe and stigma, apical view, $\times 4$; *g*, leaf base, lower side, $\times 1$; *h*, leaf middle, lower side, $\times 1$; *i*, leaf apex, lower side, $\times 1$.

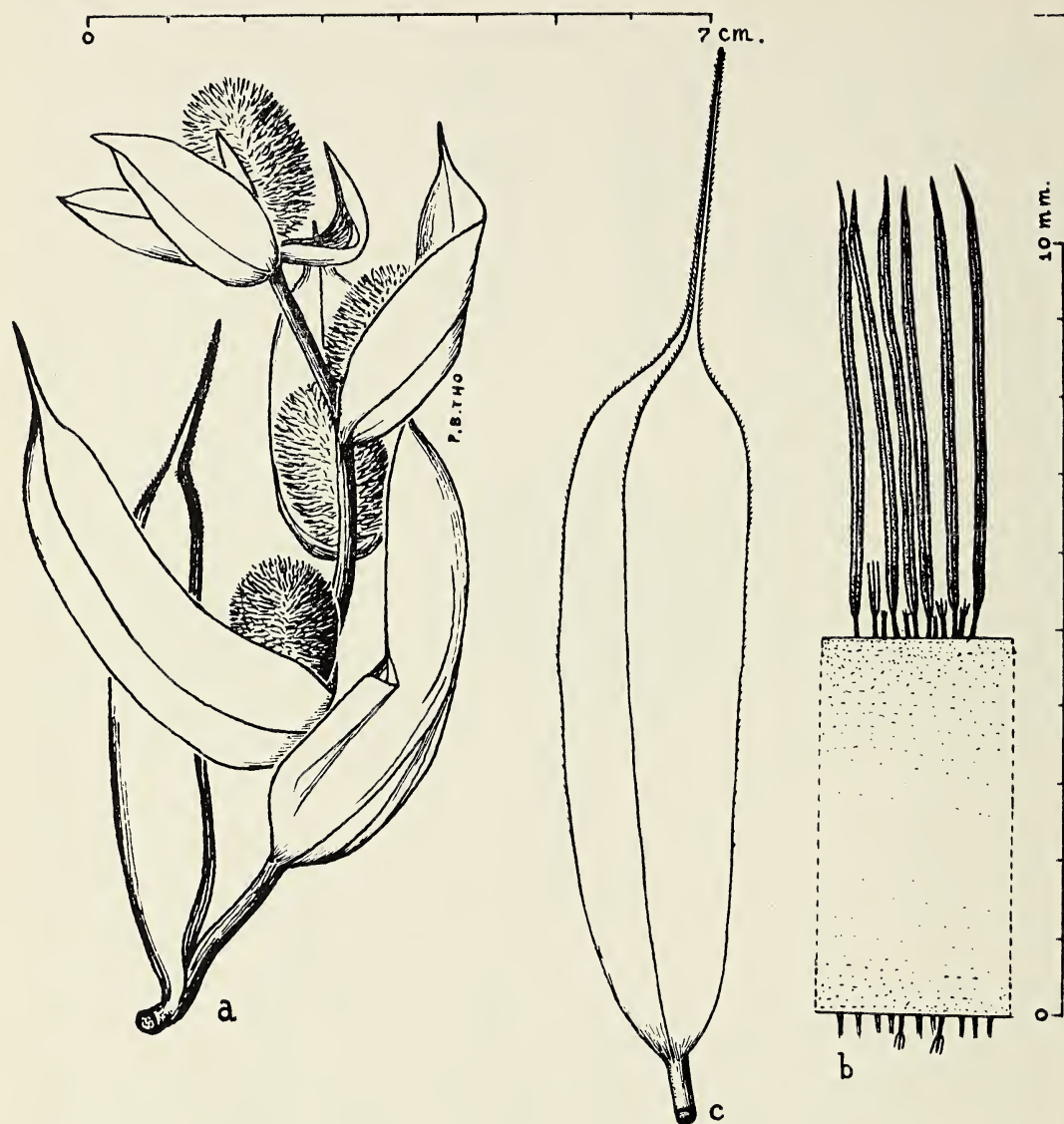


FIG. 176. *Pandanus parvus* Ridl., from Singapore, cult., 1895, H. N. Ridley. *a*, Staminate inflorescence, $\times 1$; *b*, stamens, lateral view, $\times 10$; *c*, floral bract, lateral view, $\times 1$.

EXPANDED DESCRIPTION: Pistillate stems 0.8–2.92 m tall, 6–12 mm in diameter; prop roots up to 50 cm long, 4–5 mm in diameter, smooth, green to brown, nearly vertical; leaves 27–50 cm long, 21–48 mm wide, the caudate apex 3–9 cm long; peduncle 5–12 cm long; syncarp 2.5–4 cm long, 2.5–3.3 cm in diameter, globose or ovoid-globose.

DESCRIPTION OF STAMINATE PLANT: Staminate inflorescence 15–18 cm long, bracts white and somewhat fleshy; peduncle 3–4 mm in diameter, fleshy, soon withering and caducous; lowest bracts 8–13 cm long, 26–30 mm wide, sterile, the body 6–9 cm long, navicular, with prominent parallel veins, the lower half with margins unarmed; near the apex the margins

with prickles 0.5–1 mm long, 0.3–1 mm apart, subulate, diverging or subascending; the midrib with stouter prickles 0.7–1 mm long, 0.5–1 mm apart, slightly ascending; on the caudate tip the margins and midrib below with prickles 0.5–0.9 mm long, 0.5–1 mm apart, arcuate subulate, ascending; median bracts 3–4.5 cm long, 1.6–2.4 cm wide, lanceolate, the margins and the midrib below towards apex minutely prickly; spikes 5–8 and 1.5–2.5 cm long, 0.8–1.3 cm in diameter, ellipsoid, dense; stamens very numerous, attached singly and directly to the axis; filament 0.2 mm long; anther 4.5–5 mm long, 0.2 mm wide, bearing an apical subulate prolongation of the connective 0.4–0.7 mm long.

HOLOTYPE: Singapore, Kranji, 1892, *H. N. R[idley]*, (SING). Holotype examined!

SPECIMENS EXAMINED: Singapore, Hinterindien, Dec. 16, 1905, *A. Engler* 3,862 (B); Singapore, Bidadari, 1898, *H. N. R[idley]* 9, 171 (FI); Singapore, cult., first male flowers seen, 1895, *H. N. R[idley]*, (FI, SING); without collector, ex Hb. (SING), Forest Iurong, low growing plant, Jan. 10, 1889, *Flora of Singapore* 92 (B), the holotype of *P. flagellifer*.

Malaya: Johore, Sungei Pelepah Kiri, 26 June 1928, *E. J. H. Corner* 35,556 (SING).

Pandanus perakensis Ridl., Mat. Fl. Malay Penin. 2: 231, 1907; Fl. Malay Penin. 5: 81, 1925; (sect. *Acrostigma*)

Fig. 177

DIAGNOSIS OF LECTOTYPE: (Probably aculescent); leaves 1.5–1.8 m long, 2–3.6 cm wide, subcoriaceous, light green, linear, rather abruptly narrowed to the 9 cm subulate, trigonous apex, this 10 cm down 6 mm wide, in section the blade M-shaped, at midsection with 39–41 secondary veins in each half; near the base the margins with spines 2–3 mm long, 5–13 mm apart, stout subulate, arcuate, pale, broad based, ascending; the nearby midrib below with spines 2.5–3 mm long, 6–13 mm apart, similar but even thicker subulate and reflexed; at midsection the margins with subulate-tipped serrae 0.5–1.5 mm long, 4–8 mm apart, the midrib below with prickles 0.5–1 mm long, 8–15 mm apart, subulate; near the apex the margins with

serrulations 0.3–0.5 mm long, 2–3 mm apart; the midrib below with similar ones but 2–4 mm apart; peduncle 15 cm long, 8–9 mm in diameter, straight, bracted; syncarps 3–4, spicate, crowded, 4.5–6.5 cm long, 3.5–4.5 cm in diameter, elliptic-cylindric (rarely subglobose), appearing spiny from the numerous curved ascending styles (but a few at the very base reflexed), bearing about 430 drupes; drupes 20–22 mm long, 5–6 mm wide, 4–5 mm thick, oblance-fusiform, compressed, apparently green, upper ½ free, the body 13–14 mm long, oblanceoloid, the apex truncate, pileus at last shedding, the base semiorbicular, bearing a style 6–7 mm long, stout subulate, ridge angled, gently arcuate towards apex of syncarp; stigma 4–5 mm long, linear, distal, running to the very apex; endocarp 6–7 mm long, centering in lower ⅓, ellipsoid, truncate, stramineous, cartilaginous, the sides 0.15 mm thick; apical mesocarp 3–3.5 mm long, a fat discoid cavern with a few white membranes; basal mesocarp fibrous along the margins, fleshy within.

EXPANDED DESCRIPTION: Pistillate plants with peduncle 13–15 cm long; syncarps 2–3 and 4.5–7 cm long, 3.5–5.5 cm in diameter.

LECTOTYPE: Malaya, "Perak, Maxwell's Hill"; June 1893, *H. N. R[idley]*, (SING). Lectotype examined!

SPECIMENS EXAMINED: Malaya, Pahang, Kuala Lipis, 1892, *A. S. Machado* 11,633 (SING); Kedah, Baling Hill, 21 Nov. 1941, *E. J. H. Corner & J. C. Nauen* (SING).

Pandanus spinulosus (Ridl.) comb. nov. (sect. *Acrostigma*); *P. collinus* Ridl. var. *spinulosus* Ridl., Fl. Malay Penin. 5: 79, 1925.

Fig. 178

DIAGNOSIS OF HOLOTYPE: Stem slender, just below the leaves 4 mm in diameter; leaves 67–68 cm long, 16 mm wide, subcoriaceous, green above, below paler and apparently somewhat glaucous, with a central furrow over the midrib, 2-pleated, and towards the tip the 2 pleats spinulose above, at midsection with 16–18 parallel secondary veins in each half, these prominent throughout, below the tertiary cross veins visible, remote and forming elongate meshes, the blade ligulate, in outer ⅓ tapering

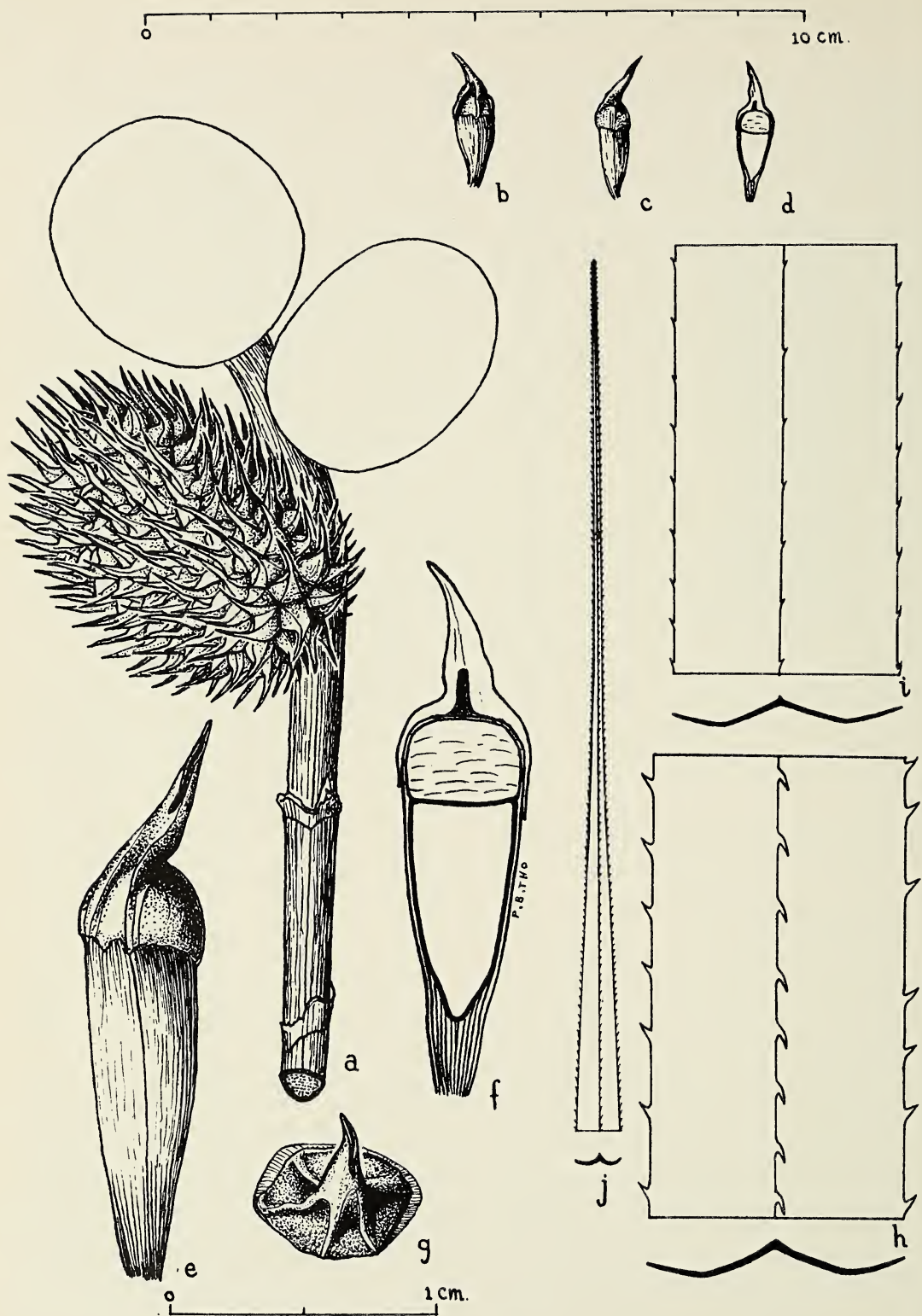


FIG. 177. *Pandanus perakensis* Ridl., from lectotype. *a*, Infructescence, $\times 1$; *b*, *c*, drupe, lateral view, $\times 1$; *d*, drupe, longitudinal median section, $\times 1$; *e*, drupe, lateral view, $\times 4$; *f*, drupe, longitudinal median section, $\times 4$; *g*, drupe, style, and stigma, apical view, $\times 4$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$.

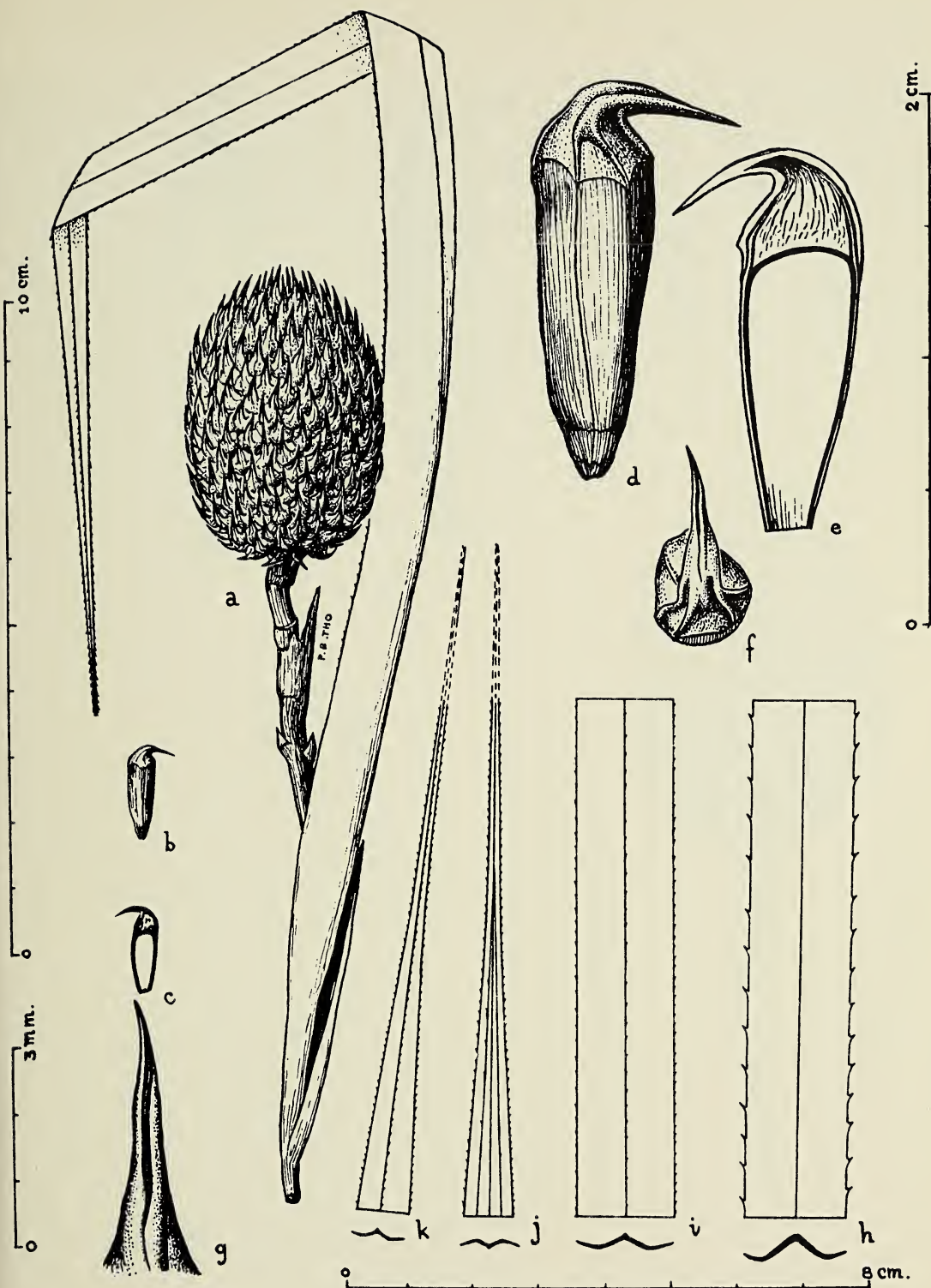


FIG. 178. *Pandanus spinulosus* (Ridl.) St. John, from holotype. *a*, Infructescence, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, style, and stigma, apical view, $\times 4$; *g*, style and stigma, lateral view, $\times 10$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, upper side, $\times 1$; *k*, leaf apex, lower side, $\times 1$.

0 3 cm.

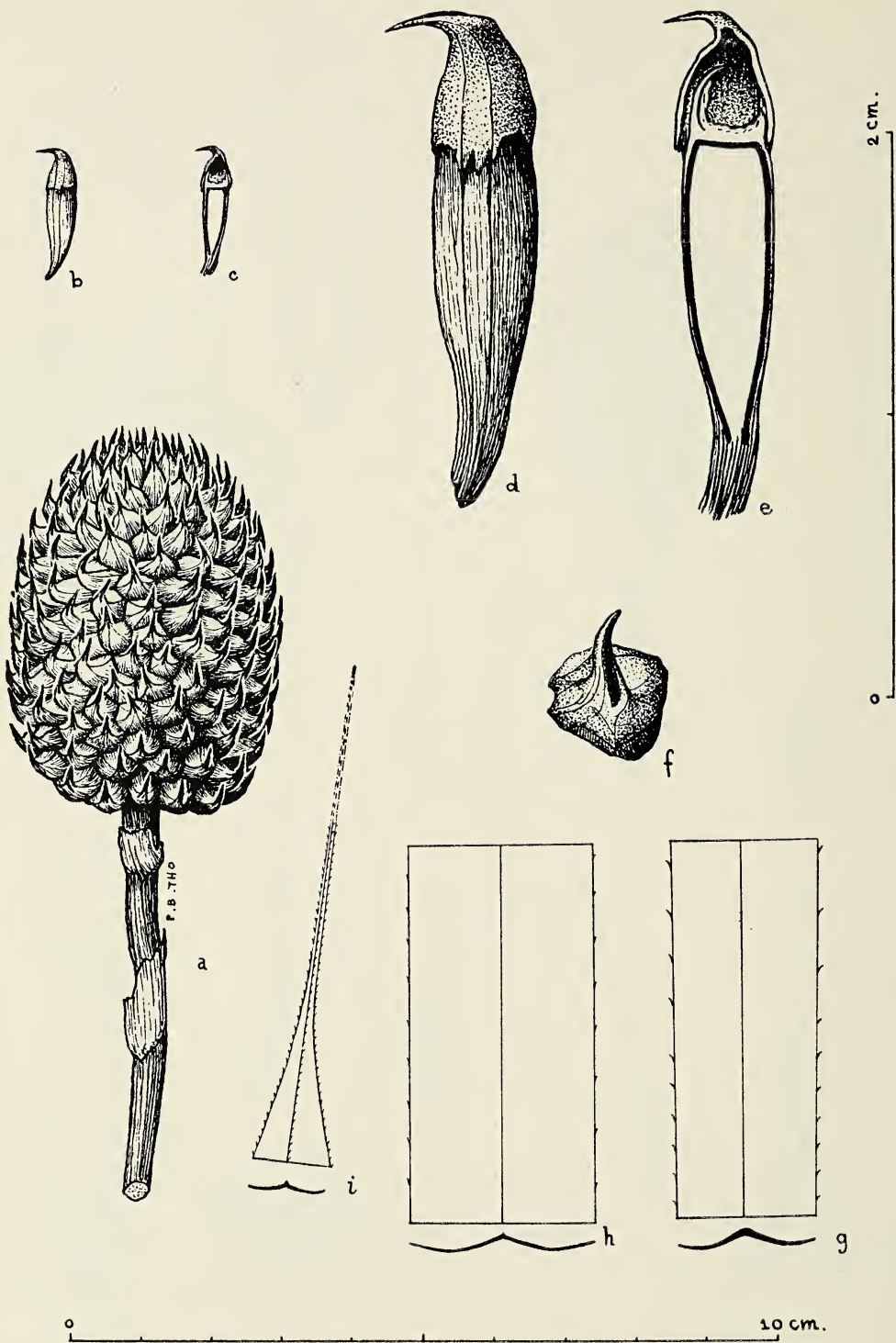


FIG. 179. *Pandanus unguiculatus* Ridl., from holotype. *a*, Syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, style, and stigma, apical view, $\times 4$; *g*, leaf base, lower side, $\times 1$; *h*, leaf middle, lower side, $\times 1$; *i*, leaf apex, lower side, $\times 1$.

gradually to the subulate, deltoid apex about 3 cm long and 1.5 mm wide, the base amplexicaul, unarmed, partly dark purple, beginning at 4 cm up the margins with prickles 0.7–1.5 mm long, 3–5 mm apart, subulate, ascending at 45°, the base thickened, pale; the midrib below unarmed to beyond the middle; at midsection the margins with prickles 0.7–0.9 mm long, 2–4 mm apart, subulate, ascending; near the tip the margins and midrib below with subulate serrations 0.4–0.6 mm long, 0.7–1 mm apart; pistillate inflorescence erect, bearing a single syncarp; peduncle 10 cm long, 4–5 mm in diameter, 3-sided, bracteate; syncarp 4.5 cm long, 3.1 cm in diameter, oblong-ellipsoid, bearing about 120 drupes, these 15–17 mm long, 3–4.5 mm wide and thick, pale green, fusiform but the upper end contracted and more slender, 5–6-angled, the body 11–12 mm long; pileus 8–9 mm long, the base 2.5–3 mm high, narrowly semiorbicular, with 5–6 sharp angles, these mostly single; style 5–5.5 mm long, sharply curved proximally, flattened and ridged below, pale, bony; stigma 3–4 mm long, distal, linear, running to the apex, brown, papillose; endocarp centering in lower $\frac{1}{3}$, but extending to the base, the walls 0.1 mm thick, cartilaginous, pale; seed 8–9 mm long, extending to the base; apical mesocarp spherical, filled with white, medullary membranes; basal mesocarp sparse, fibrous.

HOLOTYPE: Malaya, Kelantan, along the ridge of Gunong Sitong, 2,500 ft. alt., 6 March 1924, *Mohamed Nur & Foxworthy* 12,252 (SING).

DISCUSSION: *P. spinulosus* is a member of the section *Acrostigma*, and in that section is found its closest relative, *P. collinus* Ridl., which species has the leaves 25–45 cm long, 8–11 mm wide, unarmed above, each half at midsection with 10–11 secondary parallel veins, at midsection the margins with subulate-serrations 0.2–0.3 mm long; syncarp 3 cm long; drupes 14–15 mm long, the pileus base hemispheric, abruptly contracted to the subulate style which is 4–5 mm long. *P. spinulosus* has the leaves 67–68 cm long, 16 mm wide, above towards the tip the two pleats spinulose, at midsection with 16–18 secondary parallel veins in each half, at midsection the margins with subulate prickles 0.7–0.9 mm long; syncarp 4.5 cm long; drupes

15–17 mm long, the pileus base narrowly hemispheric, gradually tapering into the thick subulate style which is 5–5.5 mm long.

Pandanus unguiculatus Ridl., Mat. Fl. Malay Penin. 2: 229, 1907; Fl. Malay Penin. 5: 78, 1925; (sect. *Acrostigma*)

Fig. 179

DIAGNOSIS OF HOLOTYPE: "Plant small"; leaves 26–48.5 cm long, near the base 2–2.3 cm wide, near the middle 2.4–2.7 cm wide, ligulate, but perceptibly tapering both ways from the middle, dark green above, pale green below, thick chartaceous, only the midrib thickened, but the blade pleated and M-shaped in section, the secondary parallel veins conspicuous, at midsection 17–19 in each side, the tertiary cross veins visible in upper third below, oblique, forming short, rather oblong meshes; near the apex abruptly contracted to a subulate tip more than 20–25 mm long, 0.9 mm wide, the base amplexicaul and entire but beginning at 4–5 cm the margins with prickles 0.7–1 mm long, 2–6 mm apart, subulate, ascending, pale; the midrib unarmed for lower $\frac{2}{3}$'s; at the midsection the margins with prickles 0.5–0.7 mm long, 2–5 mm apart, subulate, appressed ascending, "red-tipped" but when dried brownish; near the apex the margins and midrib below with subulate-tipped serrulations 0.2–0.3 mm long, 0.5–2 mm apart; peduncle 5 cm or more long, 4 mm in diameter, bracted; syncarp single, 5.5 cm long, 4 cm in diameter, broad ellipsoid, bearing about 220 drupes, these 16–18 mm long (or 18–20 mm, following the curve), 4–5 mm wide, 3.5–4 mm thick, oblance-fusiform, the body 14–15 mm long, narrowly ellipsoid; the pileus smooth, pyramidal-ovoid, 5–7 mm high, tapering into the hornlike style which is 2.5–3 mm long, mostly upwards curved to about right angles; stigma 2.5–3.5 mm long, distal, linear, papillose, brown; endocarp slightly submedian, 9–11 mm long, oblanceoloid, the apex truncate, but with ascending shoulders partly surrounding the apical cavity, stramineous, cartilaginous, the lateral walls 0.15 mm thick; seed 7–8 mm long; apical mesocarp forming a broadly ovoid cavern with a few white medullary membranes; basal mesocarp scant, fibrous and fleshy.

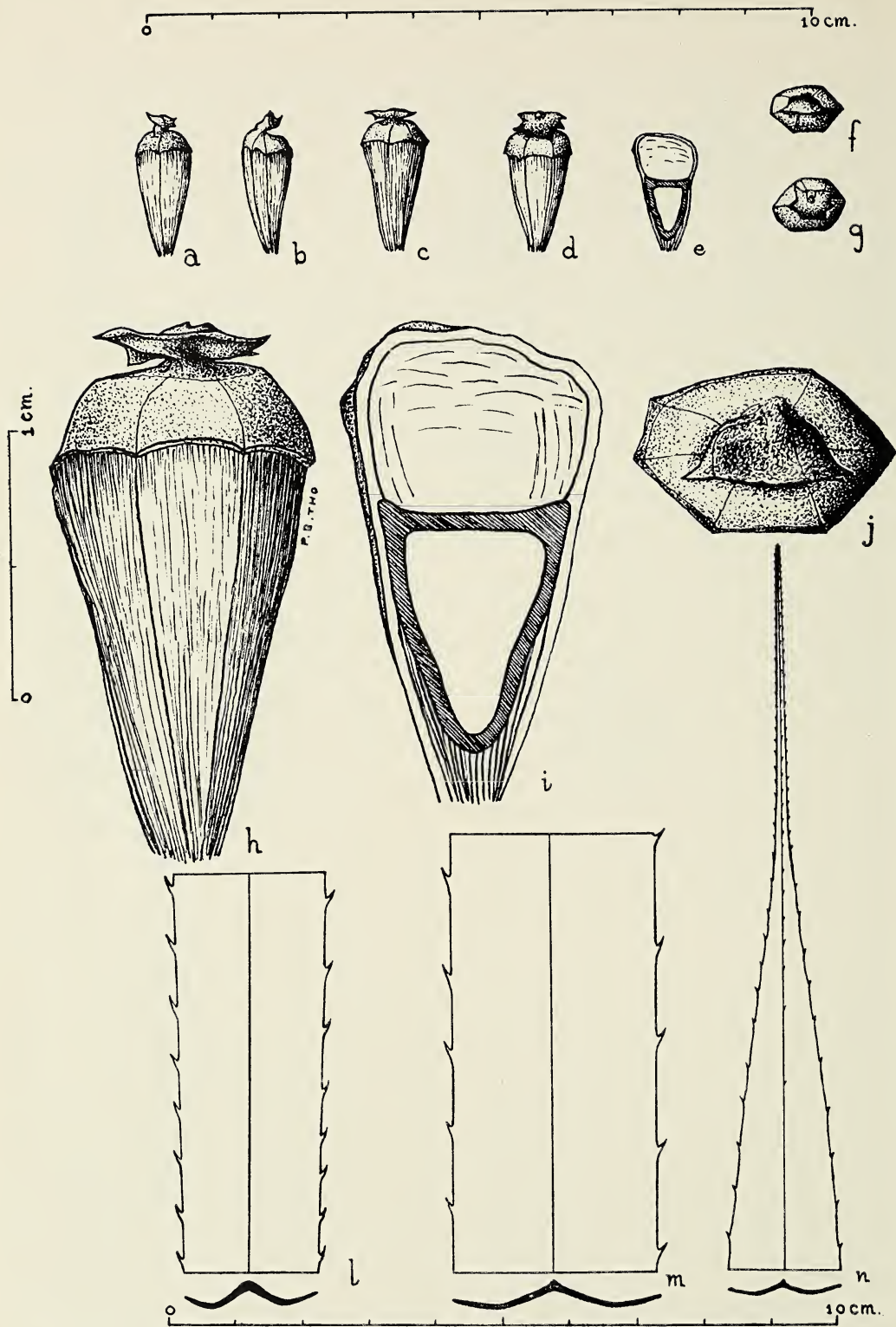


FIG. 180. *Pandanus stelliger* Ridl., from lectotype. *a-d*, Drupe, lateral view, $\times 1$; *e*, drupe, longitudinal median section, $\times 1$; *f, g*, drupe and stigma, apical view, $\times 1$; *h*, drupe, lateral view, $\times 4$; *i*, drupe, longitudinal median section, $\times 4$; *j*, drupe and stigma, apical view, $\times 4$; *l*, leaf base, lower side, $\times 1$; *m*, leaf middle, lower side, $\times 1$; *n*, leaf apex, lower side, $\times 1$.

EXPANDED DESCRIPTION FROM ALL SPECIMENS EXAMINED: Stems up to 1.8 m tall, 9–13 mm in diameter, smooth, yellowish, erect or ascending, with aerial roots; leaves arching outward and the tips pendent, glaucous below, the subulate tip 20–46 mm long; inflorescence erect; peduncle 5–6 cm long.

HOLOTYPE: Malaya, Selangor, Bukit Kutu, May 1896, *H. N. Ridley* 7,659 (SING). Holotype examined!

SPECIMENS EXAMINED: Malaya, Pahang, Fraser's Hill, 19 Aug. 1937, *E. J. H. Corner* 33,233 (SING).

SECTION *Asterostigma*

Pandanus stelliger Ridl., Roy. Asiat. Soc., Straits Branch, Jour. 41: 49–50, (1904) = 1903; Fl. Malay Penin. 5: 76, 1925; Martelli, Webbia 4(2): t. 26, f. 1–2a, 1914; (sect. *Asterostigma*)

Figs. 180, 181

DESCRIPTION OF LECTOTYPE: Shrub 1.5–3.3 m tall, the slender stems pale brown, 2.5 cm in diameter, branched, bearing a few mucros; leaves dark green, 55–60 cm long, near the base



FIG. 181. *Pandanus stelliger* Ridl., from lectotype, habit and infructescence, $\times \frac{1}{2}$.

1.8 cm wide, near the middle 2.8–3.8 cm wide, in section with a broad, central channel, and hence M-shaped, the secondary parallel veins at midsection 19–20 in each half, prominent, the tertiary cross veins visible below, transverse or oblique, forming short, somewhat oblong meshes, the actual base amplexicaul and unarmed, but beginning at 2–2.5 cm the margins with prickles 1.5–2.5 mm long, 4–9 mm apart, broad subulate, ascending, pale; the midrib unarmed except near the tip; at midsection the margins with prickles 2.1–2.5 mm long, 7–23 mm apart, similar; near the 3–8 cm apex the margins and midrib below with serrulations 0.2–0.3 mm long, 2–6 mm apart, brown; peduncle terminal, 5 cm long, leafy bracted, bearing 4 syncarps in a dense spike about 10 cm long; syncarps subequal, 5–6 cm long, 3.5–4.5 cm in diameter, ovoid to broadly ellipsoid, bearing 64–88 drupes, these 19–21 mm long (including the stigma), 7–10.5 mm wide, 6–8 mm thick, oblanceoloid with an obtusely convex apex, the sides 5–6-angled, smooth, when dried brown, the body 15–17 mm long, cuneiform; pileus 6–7 mm long, oblate semiorbicular; style subterminal, 0.5–1 mm long, vertical except on the basal drupes where sharply reflexed distally; stigmas on the expanded apical surface, 4–7 mm in diameter, 4–7-pointed, horizontal or mushroom-shaped, papillose, brown; drupe body 14–17 mm long; endocarp centering in lower $\frac{1}{3}$, bony, light brown, the inner surface shining, the lateral walls 0.5 mm thick, the apical plug 1–1.3 mm thick; seeds 6–7 mm long, obdeltoid; apical mesocarp with a cavity 6–7 mm long, with a few white membranes near the margins; basal mesocarp sparse, fibrous and fleshy.

EXPANDED DESCRIPTION OF ALL PISTILLATE PLANTS EXAMINED: Plants 1.5–4 m tall; leaves 55–113 cm long, at midsection with 19–29 secondary parallel veins in each half; peduncle 5–7 cm long, bearing 2–5 syncarps, these 4–6 cm long; drupes 7–13 mm wide, 6–10 mm thick, bright yellow.

DESCRIPTION OF STAMINATE PLANTS: Leaves 63–70 cm long, near the base 20–21 mm wide, near the middle 26–29 mm wide, at midsection the parallel secondary veins 22–24 in each half, and at midsection the margins with appressed ascending serrulations 0.3–0.4 mm long, 7–12

mm apart; staminate inflorescence 47 cm long, leafy bracted; lowest bract 47 cm long, 2.2 cm wide, for the lower 10 cm slightly distended, sheathing and paler, the rest foliaceous; floral bracts thin, apparently white, the median one 15 cm long, 4.6 cm wide, lanceolate, on the outer $\frac{1}{3}$ the margins and midrib below with serrulations 0.1 mm long, 0.2–1 mm apart; the 7 spikes 3–6 cm long, 12–15 mm in diameter, cylindric, dense; fascicle 5–8 mm long, with 19–22 stamens, the naked common column 3–4 mm long, rhachis 2–2.5 mm long, clavate; free filament tips 1–2 mm long, divergent; anthers 1.5–2 mm long, linear-oblong, bearing a pale subulate projection of the connective 0.2–0.3 mm long.

LECTOTYPE: Malaya, "Selangor, on the Tras Route at the 20th mile (8775)," 2,000 ft. elev., July 1897, *H. N. Ridley* (SING). Lectotype here designated; specimen examined! Isotype (FI)!

SPECIMENS EXAMINED: Malaya: Perak, Larut, top of mountains, open jun[gle], 2,000 to 3,000 ft. alt., April 1883, *H. Kunstler* 4,166 (CAL); Haram Parak, June 1884, *Scortechini* (CAL).

Pahang: Gunong Tahan, 7 Sept. 1937, *E. J. H. Corner* (SING); Sungei Chelia, Chagar Perah, 14 Oct. 1927, *M. R. Henderson* 19,370 (SING).

Penang: Government Hill, Dec. 1895, *C. Curtis* (SING); Waterfall Hill, 500 ft. alt., June '88, *L. Wray Jr.* 2,227 (CAL).

SECTION *Hombronia*

Pandanus irregularis Ridl., Fl. Malay Penin. 5: 76–77, 1925; Henderson, M. R., Roy. Asiat. Soc., Malay Branch, Jour. 17: 82, 1939; (sect. *Hombronia*)

Figs. 182, 183

DIAGNOSIS OF HOLOTYPE: "Leaves long, very broad," 9.3 cm wide, thick and leathery, 1-ribbed, 2-pleated, in section depressed, M-shaped, the secondary parallel veins visible below, scarcely so above and at midsection 83–92 in each half, the base amplexicaul and unarmed, but beginning at 12 cm up the margins with thorns 4.5 mm long, 1–2 cm apart, heavy deltoid subulate, black-tipped, ascending; the midrib below with similar reflexed thorns 2–3 cm apart;

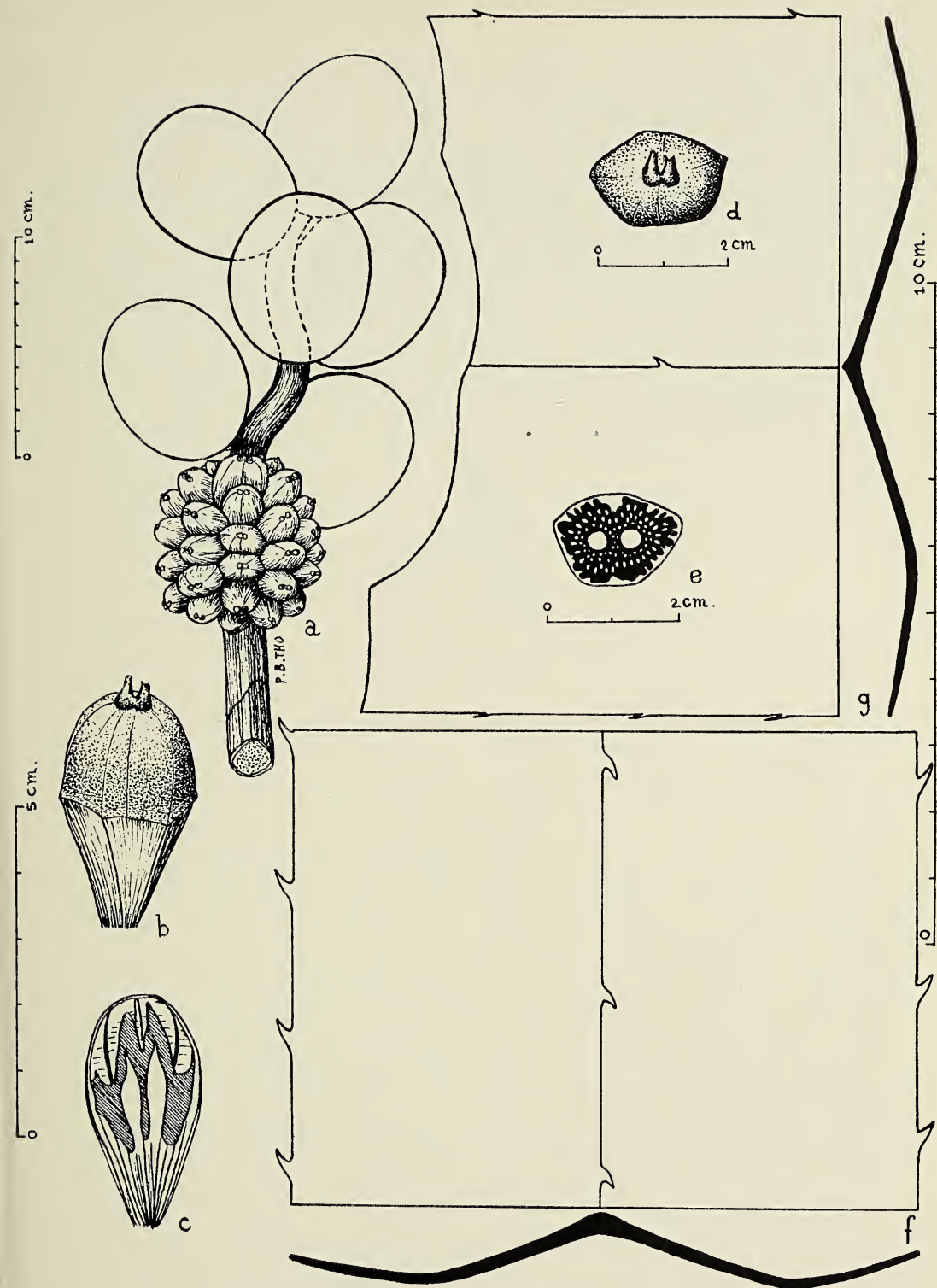


FIG. 182. *Pandanus irregularis* Ridl., from holotype. *a*, Infructescence, $\times \frac{1}{3}$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe and stigmas, apical view, $\times 1$; *e*, drupe, transverse median section, $\times 1$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$.

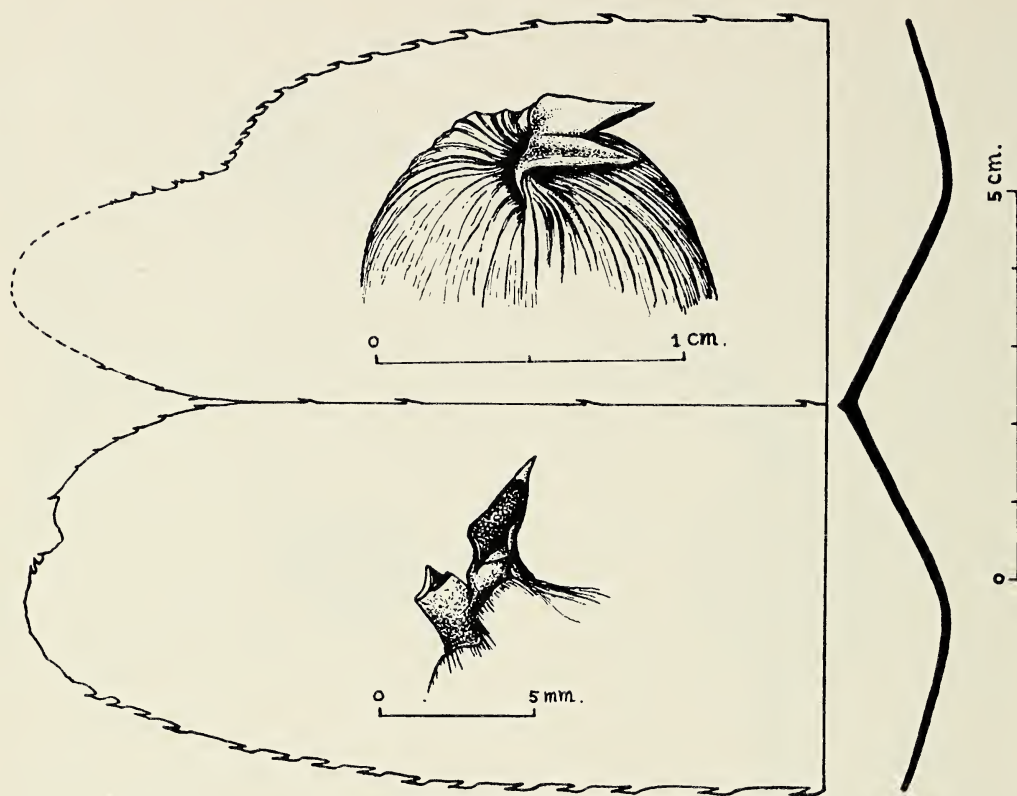


FIG. 183. *Pandanus irregularis* Ridl., from holotype, leaf apex, lower side, $\times 1$.

on a leaf section cut higher up (exact place unknown) the margins with spines 3–3.5 mm long, 25–36 mm apart, heavy subulate, ascending; the midrib below with scars of fallen spines 3–6 cm apart; pistillate inflorescence 30 cm long, with about 7 syncarps; peduncle 15 mm in diameter, obtusely trigonous, bracted; syncarps 6.5–7.5 cm long, subglobose, bearing about 36–44 drupes, these 1–3- but mostly 2-celled, 3–3.5 cm long, 1.8–2.4 cm wide, 1.2–1.5 cm thick, "dark green," narrowly obovoid to oblanceoloid, compressed, the apex entire, obtuse, the sides smooth, convex, lateral sutures none; stigmas almost all eroded but 1 basal drupe bears a single stigma 5 mm long, lanceolate, sharply bent to the horizontal, the receptive surface distal; endocarp 22 mm long, centering in upper $\frac{2}{3}$, at midsection filling the drupe, bony, massive, dark brown but including pale fibers, the lateral walls 4–5 mm thick; seeds

8–9 mm long, 3 mm in diameter, ellipsoid; apical mesocarp cavernous, with strong, longitudinal fibers and soft pith; basal mesocarp fibrous and fleshy.

EXPANDED DESCRIPTION OF ALL SPECIMENS EXAMINED: Leaf more than 1.4 m long, near the base 9 cm wide, near the middle 12 cm wide, near the apex 10.5 cm wide, broad ligulate; margins near the base with thorns 3.5–4.5 mm long, 1–2.5 cm apart; midrib below with thorns 3–3.5 mm long, 2–5 cm apart, subulate, reflexed; at midsection the margins with spines 4–4.5 mm long, 20–25 mm apart, sharply ascending, subulate but the base much thickened; the midrib below concealed; the apex apparently damaged in growth and without a caudate apex, rather contracted to 2 broadly obtuse lobes and deeply emarginate, and even prickly on the margins of the cleft, all this, however, apparently an abnormality; peduncle 30 cm long;

spike 14 cm long, bearing 4 syncarps; stigmas 4 mm long, sharply proximally bent, the receptive surface usually proximal.

HOLOTYPE: Malaya, Kelantan, Sungei Ketah, Batu Bau (Bow), 15 Feb. 1924, *Mohamed Nur & Foxworthy 12,104* (SING). Holotype examined!

SPECIMENS EXAMINED: Malaya, Pahang, Gua Tipus, the common pandan on the limestone, 17 Oct. 1927, *M. R. Henderson 19,468* (SING).

DISCUSSION: *P. irregularis* was placed by Dr. Ridley in the section *Rykia*. It has, however, the drupes 1–3-celled, and usually 2-celled, with the cells in linear arrangement, and the large stigmas terminal, but distal and laterally directed. There is no question but that it must now be placed in the section *Hombronia*.

It is one of the numerous plant species known to occur only on limestone knobs. These precipitous pinnacles or narrow ridges rise spectacularly from the rolling uplands of Thailand and Malaya. Their sides are often precipices of shining, white limestone, sparsely vegetated, but their crests have a dark evergreen, virgin forest cover. To a botanist they are very attractive. Four species of *Pandanus* in Malaya are restricted to these calcareous habitats. Besides this species published by Ridley, two more are now being described, and one more has yet to be found in fruit. A good account of this localized flora is given by Dr. M. R. Henderson (Roy. Asiat. Soc., Malay Branch, Jour. 17: 13–87, pl. III–XI, 1939).

Malaya, SECT. NOV.

Phalangibus pluricarpellatis, stylis terminalibus adscendentibus vel arcuatis corniformatis integris vel bifidis, stigmatibus centripetalibus ellipsoideis vel lanceolatis; plantis masculis inconnitis.

Phalanges of several united carpels; styles terminal, ascending or arching, stout, hornlike with

a subulate apex or compressed and more or less oblong, with the apex sharply bifurcate; stigmas centripetal, ellipsoid or lanceolate; staminate plants unknown.

HOLOTYPUS: *Pandanus Klossii* Ridl., Fed. Malay States Mus., Jour. 6: 190–191, 1915.

DISCUSSION: The single known species occurs on the mountains of Pahang in Malaya. It combines the characteristics of the section *Rykia* in its hornlike, simple or bifurcate styles, and of the section *Pandanus*, in its many-carpellate, large phalanges. Since these two sections are very distinct and are only remotely related, it is best to make the very bizarre *P. Klossii* the basis of a new section.²

Pandanus Klossii Ridl., Fed. Malay States Mus., Jour. 6: 190–191, 1915; Fl. Malay Penin. 5: 74, 1925; (sect. *Malaya*)

Figs. 184, 185

DIAGNOSIS OF HOLOTYPE: Shrub 2–7 m tall; stems usually solitary, 7.5 cm in diameter, gray, erect or arcuate; leaves 1.3–1.8 m long, 6.8–7.2 cm wide, thick coriaceous, above dark green, below pale green, 1-ribbed, but 2-pleated and in section low M-shaped, the longitudinal parallel secondary veins 0.5–0.8 mm apart, 49–52 in each half, evident on both sides as are the tertiary cross veins that form a network of meshes, oblong or rhombic, longer than broad, the blade ligulate, and only near the tip rather abruptly narrowing to a 5 cm stout subulate tip, trigonous and 2–3 mm wide, the very base not collected, near the base the margins with stout thorns 5–8 mm long, 8–30 mm apart, arcuate ascending, black; the midrib below with similar but reflexed thorns; at midsection the margins with prickles 3 mm long, 15–50 mm apart, subulate, ascending, flat appressed; the midrib below with prickles 2 mm long, 35–50 mm apart, heavy, arcuate, ascending; near the tip

² The new section can be inserted in the author's key in this Revision of the Genus *Pandanus* (p. 2) by replacing the 11th line from the bottom by:

- L. Stigmas elongate, acerose, or stout hornlike, simple or bifurcate,
 - a. Stigmas stout hornlike, simple or bifurcate.....*Malaya*
 - a. Stigmas elongate, acerose,

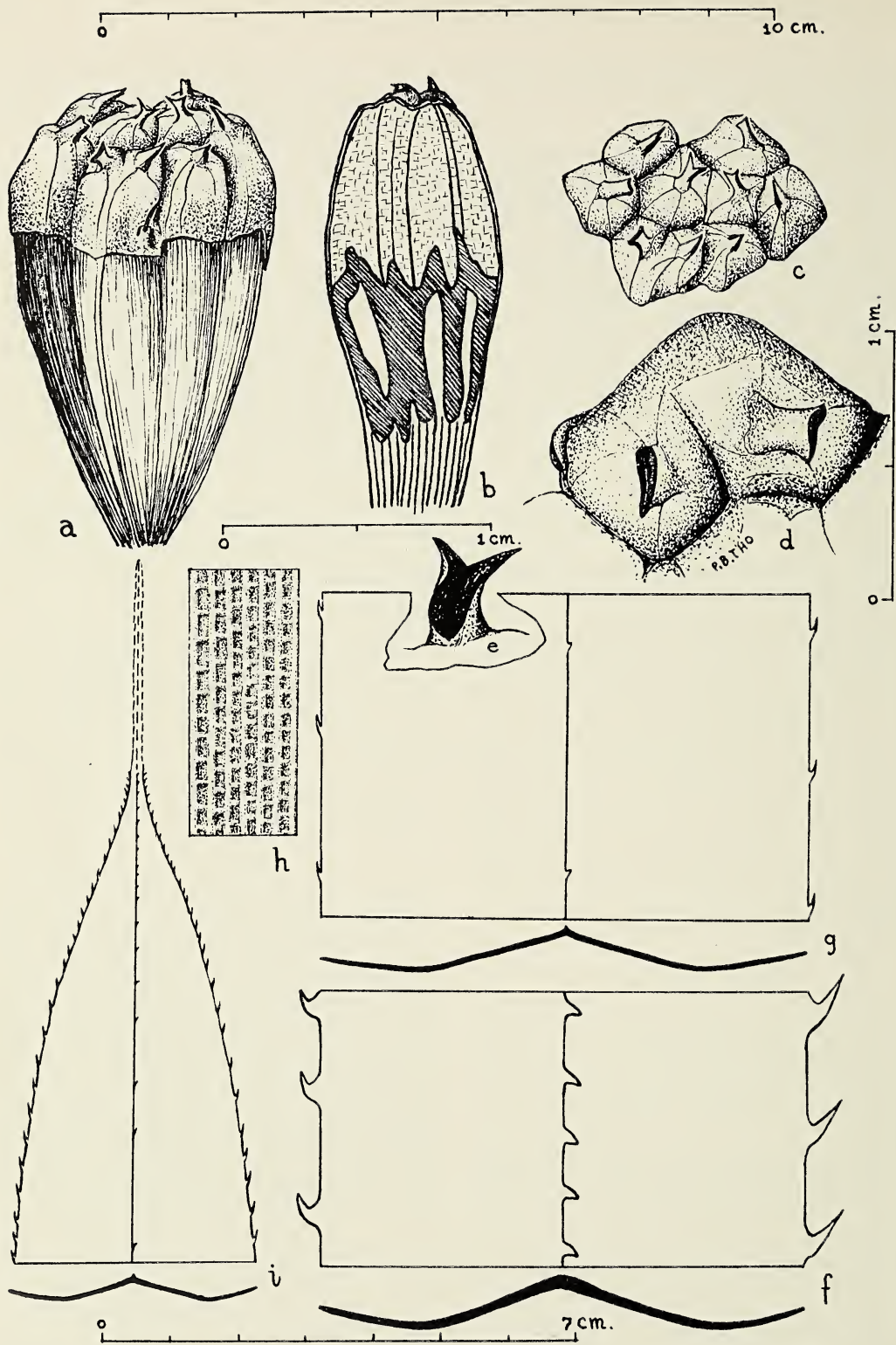


FIG. 184. *Pandanus Klossii* Ridl., from holotype. *a*, Phalange, lateral view, $\times 1$; *b*, phalange, longitudinal median section, $\times 1$; *c*, phalange, and stigmas, apical view, $\times 1$; *d*, carpel apices and stigmas, apical view, $\times 4$; *e*, style and stigma, oblique view, $\times 4$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$; *h*, venation in outer third, lower side, $\times 4$; *i*, leaf apex, lower side, $\times 1$.

the margins and midrib below with serrations 0.3–0.5 mm long, those of the margin 1–1.5 mm apart, those of the midrib below 2–5 mm apart; pistillate peduncle 15–30 cm long, 12–18 mm in diameter, 3-sided, leafy bracted; syncarp single, globose or ellipsoid, about 15 cm in diameter; phalanges numerous and 6–6.5 cm long, 3.6–3.9 cm wide, 2–2.7 cm thick, cuneiform, 4–6-angled, "showing signs of turning red or orange," the sides smooth, gently convex, free in upper $\frac{1}{3}$, the apex low convex, lateral sutures visible only in upper $\frac{1}{3}$; central apical sinuses 1–4 mm deep, straight or arcuate, narrow; carpels 9–10 (in a double 16–17 and the phalanges 5.7–6 cm wide), the apices semiorbicular, faintly angled; styles 4–6 mm long, dark, bony, either simple and hornlike or flattened and sharply bifid, mostly centripetal; stigmas as long as the styles, ellipsoid or lanceolate, brown, papillose, covering the proximal face; proximal sinus none; endocarp in lower $\frac{1}{3}$ and 2.7 cm long, bony, massive, dark-brown, the lateral walls 2 mm thick, the inner surfaces shining and rugulose; seeds 14–16 mm long, 2–3 mm in diameter, oblong-ellipsoid; upper mesocarp 2–2.5 cm long, of dense pith and a few fibers; basal mesocarp fibrous and fleshy.

ADDED DESCRIPTION FROM ALL SPECIMENS EXAMINED: Phalanges about 96; carpels 5–10; syncarp 9–15 cm in diameter.

HOLOTYPE: Malaya, Pahang, Gunong Tahan, July 1911, *H. N. Ridley* 16,037 (SING). Isotype (BO). Ridley stated, "Common all over the Padang. In the more open exposed spots the stem is short and erect, about 6 to 8 feet tall; in the woods the stems are long and weaker, often falling about at all angles, 20 feet or more long. No trace of male flowers could be seen anywhere. The plant is very abundant, almost filling up the woods in some places." The collection, *Ridley* 16,037, was made by Ridley previous to his publication of the species in 1915, was labeled *P. Klossii* by him, and seems to have been the only collection in the Singapore herbarium up to that time. In his *Flora of the Malay Peninsula* (1925) he accepted the species and cited only his collection from Gunong Tahan, so this one seems acceptable as his holotype.

SPECIMENS EXAMINED: Malaya, Pahang,

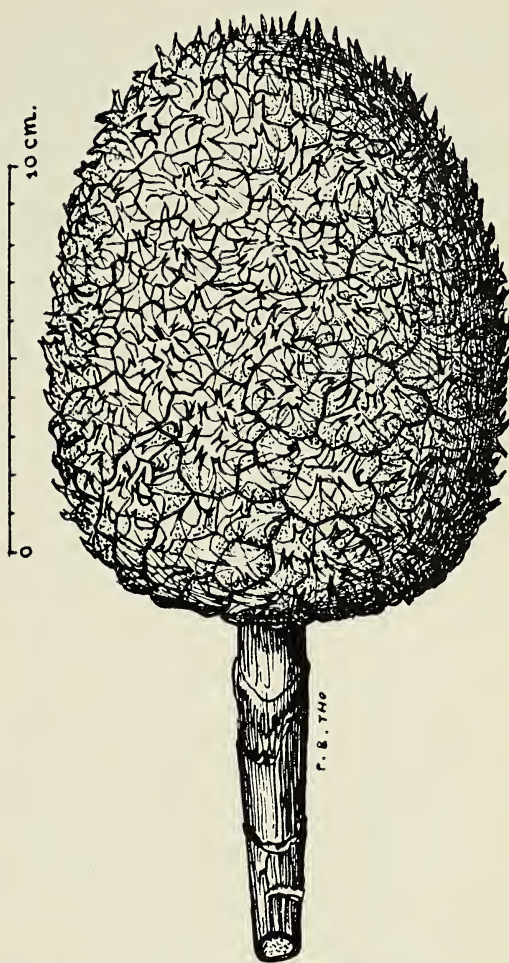


FIG. 185. *Pandanus Klossii* Ridl., from holotype, syncarp, $\times \frac{1}{2}$.

Gunong Tahan, 14 Sept. 1937, *E. J. H. Corner* (SING); Pahang, Gunong Tapis, Kuantan, 4,600 ft. alt., 14 June 1934, *C. F. Symington & Kiah* 28,843 (SING).

DISCUSSION: *P. Klossii* Ridl., a very unique species, is here made the holotype for the new section *Malaya*. This combines the characters of the two sections *Pandanus* and *Rykia*. When Ridley described the species in 1915 he did not place it in a section, but later in 1925 in his *Flora of the Malay Peninsula* he put it in the section *Keura*, which is now called *Pandanus*. As usual he had a good eye for species, but his description seems to have been hastily drawn. He stated (1915: 191) "the drupes are separate

till the fruit is nearly ripe, when from 6 to 7 become adnate and remain so as the whole fruit breaks up." The holotypic collection consists of two sheets, one with overripe fruit, the other with a small, immature syncarp. In both the phalanges are of several fused carpels. The carpels are fused from the base to within 4 mm of the apex, and the sides lack sutures. The writer sees no evidence on these specimens to confirm Ridley's statement that the drupes are separate and only tardily connate; on the contrary, all the structural evidence indicates that the phalanges are of several carpels united from the beginning.

Though Ridley did not explain the source of his specific epithet, it was obviously given in honor of Cecil Boden Kloss, an English zoologist and to a lesser degree a botanist. In 1903 and 1907 he was employed by the Singapore Botanic Garden. He was later director of the Raffles Museum.

Multidens, SECT. NOV.

Frutices, foliis angustis, syncarpio solitario elipsoideo, stylo singulo terminali osseoso proxime curvato basi cylindrico margine (2-) 3-6-lobato lobis deltoideis, drupis 1-loculatis. Plantis masculis cum inflorescentia bracteata 1-spicata, staminibus distinctis in axilli affixis, filamentis 4-plo tam longis quam antheris.

Bushes; leaves narrow; syncarp solitary, elipsoid; style single, terminal, proximally curved, bony, shining, the base cylindric, the margin (2-) 3-6-lobed, the lobes deltoid; drupes 1-celled. Staminate plants with inflorescence bracteate, bearing a solitary terminal spike; stamens separate, attached directly to the axis; filament 4 times as long as the anthers.

HOLOTYPE: *P. pentodon* Ridl., Fl. Malay Penin. 5: 75, 1925. Also in the section is *P. tetradon* Ridl. of Singapore.

Pandanus pentodon Ridl., Fl. Malay Penin. 5: 75, 1925; (sect. *Multidens*)

Fig. 186

DIAGNOSIS OF LECTOTYPE: Stem short, branched, up to 2 cm in diameter; leaves said to attain more than 100 cm in length, 11-12 mm wide, coriaceous, dark glossy green, pale green beneath, channeled above the midrib and with 2 lateral pleats, in section low M-shaped, narrowly ligulate, outer halves of leaves missing, at midsection with 17-22 secondary parallel veins in each half, the tertiary cross veins barely visible below near the base, the base amplexicaul and unarmed, apparently copper-colored, beginning at 3-5 cm up the margins with pale serrulations 0.5-0.8 mm long, 1-6 mm apart; the midrib unarmed to at least beyond the middle; at midsection the margins with slender serrulations 0.3-0.6 mm long, 4-8 mm apart, the upper surface unarmed; the apex tapering to a 10 cm trigonous subulate tip which 10 cm down is 4 mm wide, the margins and midrib below with serrations 0.2-0.3 mm long, 0.7-3 mm apart; pistillate peduncle 13 cm long, 8 mm in diameter, bracted, bearing a single, erect syncarp; the highest peduncular bract 30 or more cm long, at base 2.2 cm wide, narrowly lanceolate and tapering noticeably right from the base, the margins with serrulations similar to those of the leaves, but on the upper surface beginning 10 cm up the 2 lateral pleats with similar serrulations, the lower ones 5-13 mm apart, the upper ones 2-5 mm apart; partly hiding the fruit are 3 series of floral bracts, 3 deep, and subequal, 5 cm long, 2 cm wide, lance-elliptic, fleshy, cream-colored; syncarp 5 cm long, 3 cm in diameter, bearing about 400 drupes (when young these are cream-colored), 12-13 mm long, 2-3.5 mm wide and thick, linear-oblongoid, 5-6-angled, the body 10-11 mm long, the summit rounded; pileus 2.5-3

Insertion in Key

On p. 225 (p. 2 of reprint) for the second J, read

- J. Styles 1 (-2), often cartilaginous or bony,
 - z. Styles toothlike to broad subulate, entire or bifid; staminate spikes bearing stamens fasciated at apex of column.....*Rykia*
 - z. Style with cylindric base, then curving proximally and the margin (2-) 3-6-lobed with deltoid lobes; staminate spike solitary, bearing separate stamens attached directly to the axis.....*Multidens*

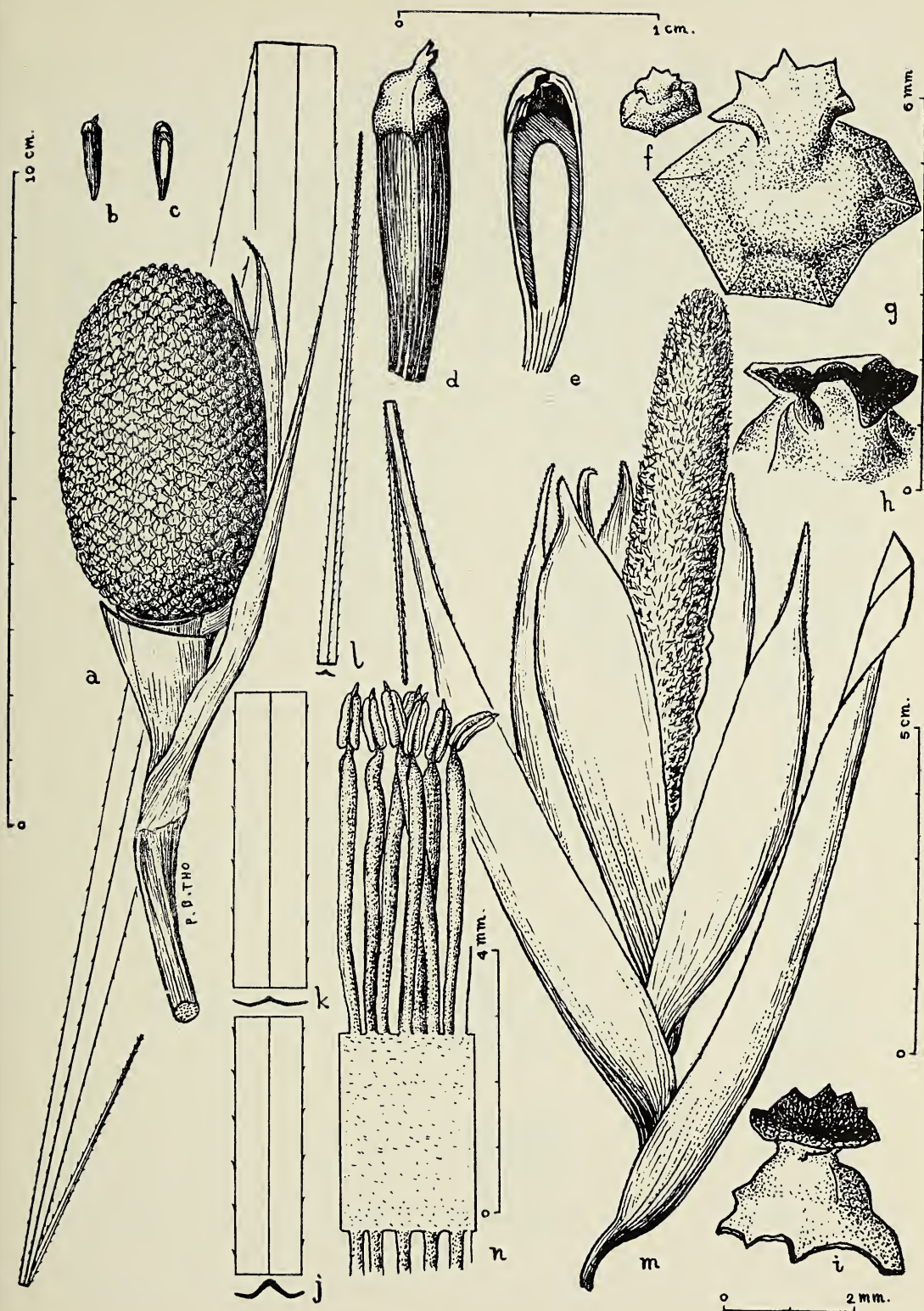


FIG. 186. *Pandanus pentodon* Ridl., from lectotype. *a*, Infructescence, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe and style, apical view, $\times 1$; *g*, drupe apex and style, apical view, $\times 10$; *h*, stigma, oblique view, $\times 10$; *i*, drupe apex, style, and stigma, lateral view, $\times 10$; *j*, leaf base, lower side, $\times 1$; *k*, leaf middle, lower side, $\times 1$; *l*, leaf apex, lower side, $\times 1$; *m*, staminate inflorescence, $\times 1$; *n*, stamens and axis, $\times 10$.

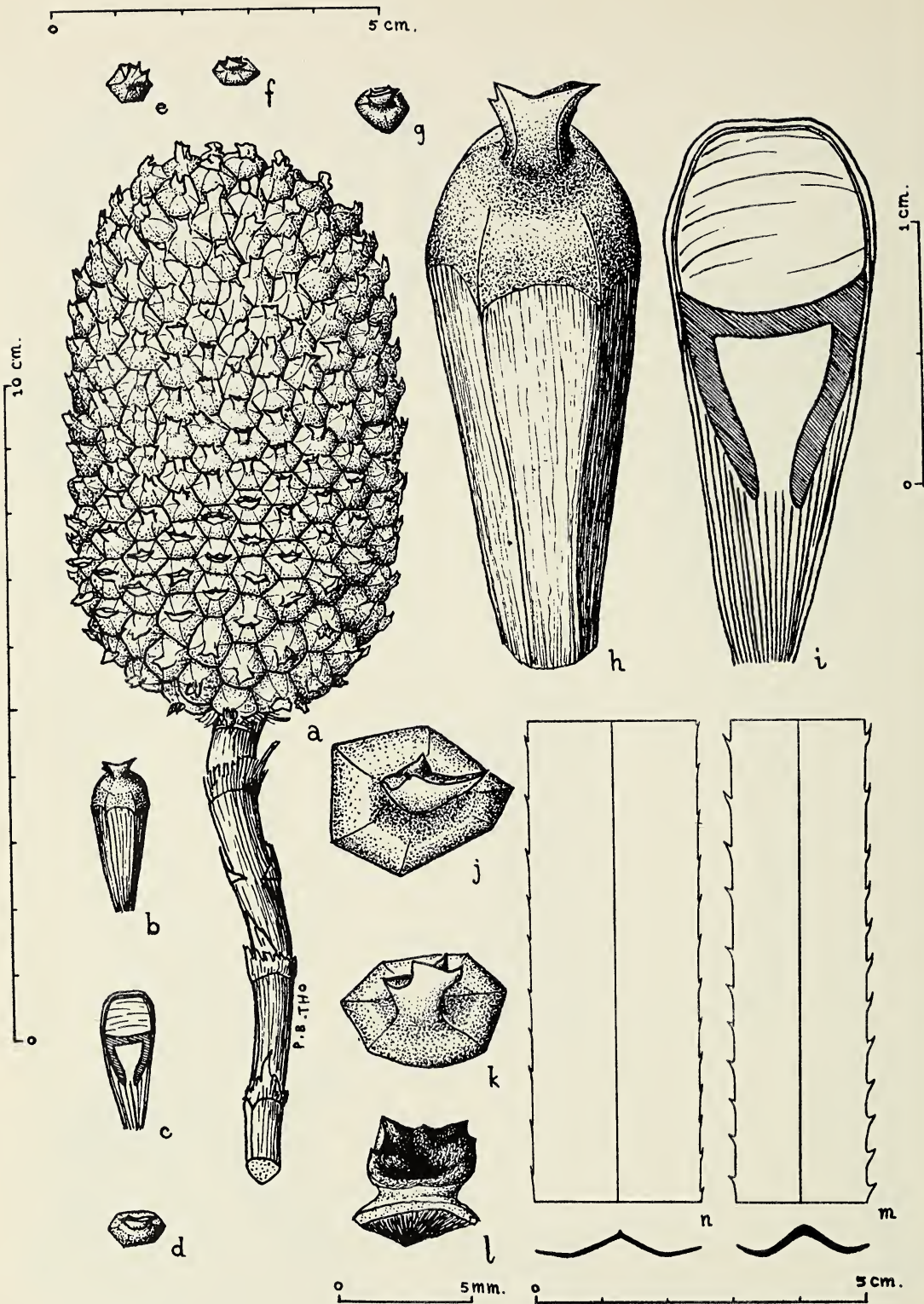


FIG. 187. *Pandanus tetradon* Ridl., from holotype. *a*, Syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d-g*, drupe, style, and stigma, apical view, $\times 1$; *h*, drupe, lateral view, $\times 4$; *i*, drupe, longitudinal median section, $\times 4$; *j, k*, drupe, style, and stigma, apical view, $\times 4$; *l*, stigma, proximal view, $\times 4$; *m*, leaf base, lower side, $\times 1$; *n*, leaf middle, lower side, $\times 1$.

mm long, the base pyramidal-semiorbicular, smooth, when dried somewhat yellowish; style 1–1.5 mm long, apical, bony, yellowish, shining, its base short cylindric, then the rest sharply curved proximally and flabellate with the margins (3–) 4–5 (–6) dentate; stigma 0.5–1 mm long, obdeltoid to flabellate, papillose, brown, on the distal side of the style; endocarp central, bony, pale brown, the upper lateral walls 1 mm thick; seed 5–5.5 mm long; apical mesocarp an empty cavern; basal mesocarp fibrous up the sides, fleshy within.

STAMINATE PLANT: Herbage not seen; staminate inflorescence dense, leafy bracted, the main part 14 cm long; lowest floral bract about 30 cm long, the upper part green, foliaceous, 10 mm wide, with serrulations 0.2 mm long, 2–5 mm apart, the 10 cm basal part 19–20 mm wide, folded, firm, apparently pale, with similar or smaller serrulations; median floral bract 7 cm long, 3 cm wide, navicular, elliptic, acute, serrulate near the apex on margins and midrib below, firm, apparently pale; spike single, terminal, 7.5 cm long, 13 mm in diameter, cylindric, dense; stamens distinct, attached directly to the axis; filaments 4.2–4.4 mm long, anthers 0.8 mm long, narrowly oblong, bearing at tips a 0.15–0.2 mm subulate prolongation of the connective.

LECTOTYPE: Malaya, Johore, Ulu Kahang, abundant along edges of Kahang river, 250 ft. alt., 1 June 1923, *R. E. Holttum 10,861* (SING)—the pistillate plant here designated as lectotype. Mingled on the same sheet is a staminate plant.

Pandanus tetradon Ridl., Roy. Asiat. Soc., Jour. 68: 13–14, 1915; *P. singaporensis* Kanehira, Jour. Jap. Bot. 14: 173–177, figs. 6–8, 10, 1938, a superfluous name; non *Barroetia tetradon* Gaud., Bot. Voy La Bonite, t. 13, figs. 1–8, 1841, an invalid name; non *P. tetradon* Balf. f., Linn. Soc. Bot. Jour. 17: 63, 1878, a name not accepted by its author; non *P. tetradon* Balf. f. ex Kanehira, Bot. Mag. Tokyo 52: 236–239, fig. 70, 1938, a later synonym of *P. compressus* Martelli (1905); (sect. *Multidens*)

Fig. 187

DIAGNOSIS OF HOLOTYPE: "Large bushy plant; branches at apex 2.5 cm in diameter"; leaves well over 97 cm long, 2.6 cm wide at the middle, 2 cm wide near the base, coriaceous, 1-ribbed, 2-pleated, in section low M-shaped, about at the midsection with 25–26 secondary parallel veins in each half, these visible at least below throughout, tertiary cross veins visible in outer half, transverse, forming oblong meshes, mostly short, the blade ligulate, the apex not preserved, the base amplexicaul, unarmed, beginning at 5 cm up the margins with prickles 1.5–2.5 mm long, 5–10 mm apart, subulate-tipped serrae, pale, with reddish tips; the midrib below unarmed for at least lower $\frac{2}{3}$'s; near the midsection the margins with similar serrae, 1.3–1.5 mm long, 6–13 mm apart; leaf apex "acuminate," but not preserved; pistillate inflorescence terminal, more or less concealed; peduncle 19 cm long, 7 mm in diameter, 3-sided, sinuous, leafy bracted, bearing 1 syncarp, this 8.8 cm long, 5 cm in diameter, cylindric with obtuse ends, bearing about 176 drupes, these 22–24 mm long, 6–10 mm wide, 5–10 mm thick, increasing upwards in size and the apical ones definitely the largest, cuneate-oblancoeloid, obtuse, 5–6-angled, upper $\frac{1}{3}$ free, the sides nearly smooth; style 3–4 mm long, bony, dark shining brown, at base cylindric, then quadrate and curved proximally, and all the lateral ones with an oblique plane to the 2–3–4-dentate margins; stigma 1–2 mm wide or long, rugose, of various shapes, filling the cavity proximal of the style apex, with 2–4 (–5) deltoid lobes; endocarp centering in lower $\frac{5}{8}$, bony, dark brown; seed 6 mm long, obdeltoid; apical mesocarp 6–7 mm long, a rounded cavity with a few pale membranes; basal mesocarp fibrous and fleshy.

EXPANDED DESCRIPTION OF PISTILLATE PLANTS: Stems at apex 1.5–2.5 cm in diameter, brown, striate, covered with ascending adventitious rootlets 1–2 cm long; leaves 78 to more than 97 cm long, the tip gradually diminishing to a trigonous subulate apex about 10 cm long, and at base 4 mm wide, on the subulate apex the margins and midrib below with serrations 0.3–0.5 mm long, 2–5 mm apart; syncarp single or with a secondary one below and 4.5 cm long, ovoid.

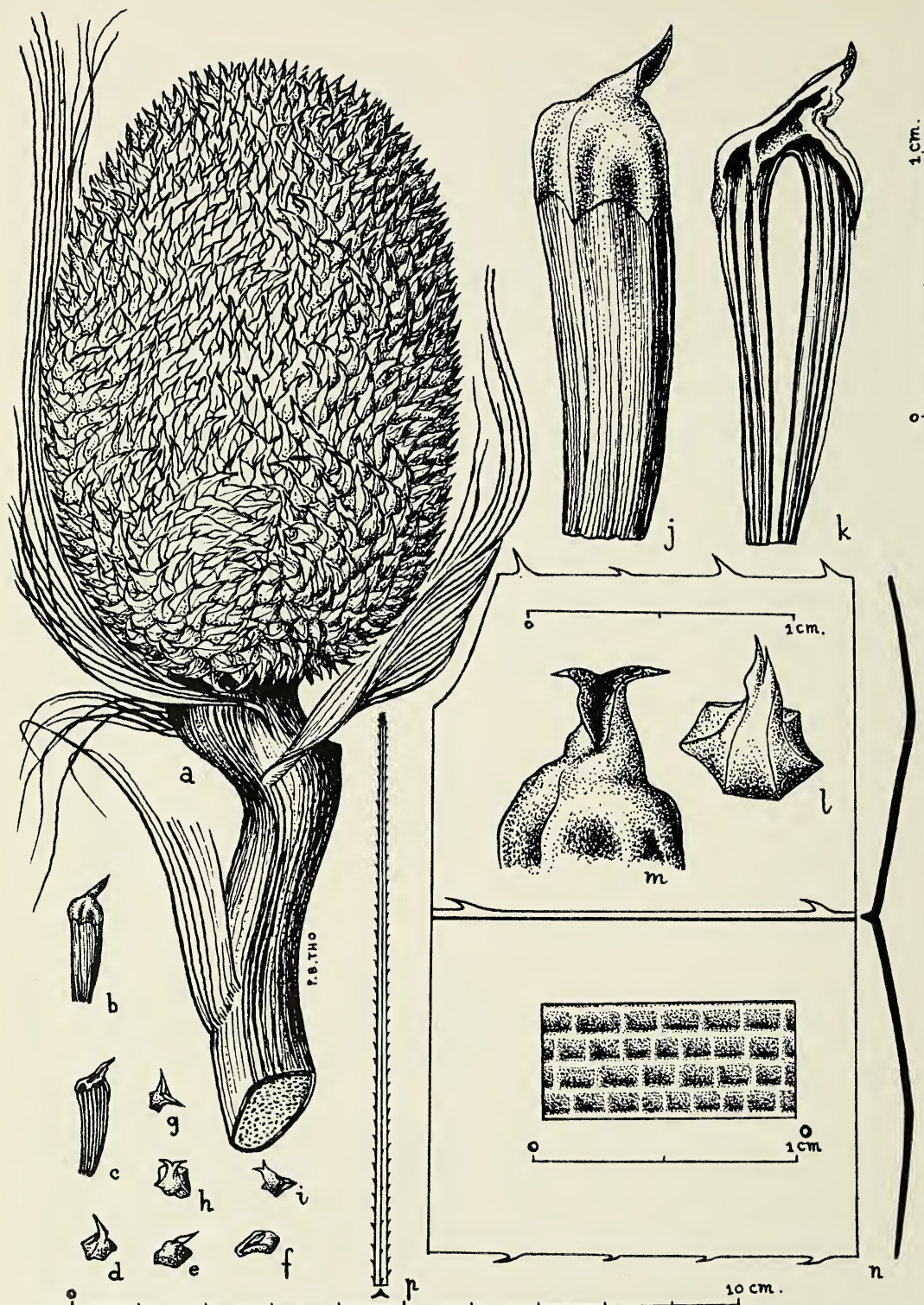


FIG. 188. *Pandanus immersus* Ridl., from holotype. *a*, Syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d-i*, drupe, style, and stigma, apical view, $\times 1$; *j*, drupe, lateral view, $\times 4$; *k*, drupe, longitudinal median section, $\times 4$; *l*, drupe apex and style, apical view, $\times 4$; *m*, drupe apex, style, and stigma, proximal view, $\times 4$; *n*, leaf middle, lower side, $\times 1$; *o*, venation of leaf middle, lower side, $\times 4$; *p*, leaf apex, lower side, $\times 1$.

HOLOTYPE: Singapore, on the west coast road near Pasir Panjang, Dec. 11, 1911, *H. N. Ridley* 15,465 (SING). Holotype examined!

SPECIMENS EXAMINED: Singapore, Botanic Gardens, Aroid Rockery, cult., 20 April 1936, *E. J. H. Corner* 30,993 (KEP, SING).

SECTION *Rykia*

Pandanus immersus Ridl., Asiat. Soc., Straits Branch, Jour. 41: 48–49, 1903; Mater. Fl. Malay Penin. 2: 224, 1907; Fl. Malay Penin. 5: 76, 1925; Martelli, Webbia 4(1): 18, 1913; (sect. *Rykia*)

Fig. 188

NOM. VERN.: "mengkuang ayer."

DIAGNOSIS OF HOLOTYPE: Aquatic, "the stem rising but little above" the surface of the river; leaves "many feet long," 10.2 cm wide, coriaceous, green above, pale and glaucous beneath, the longitudinal veins strong, visible above and conspicuous below, about 1 mm apart, at midsection with 70 secondary parallel veins in each side, the venation also consisting of tertiary cross veins 1–3 mm apart, these easily visible above and conspicuous below, the base not preserved but the blade 1-ribbed, 2-pleated, in section M-shaped, ligulate, narrowing upwards and in the upper quarter tapering to a subulate deltoid apex about 30 cm long, and at a point about 10 cm down from the tip only 1.3 mm wide; at about the midsection the margins with thorns 2.5–4 mm long, 9–18 mm apart, subulate but the base thickened, nearly straight, ascending, pale except for the very tip which may be reddish; near the tip the margins with serrae 0.8–0.9 mm long, 1.5–3 mm apart, stout; the midrib below nearly unarmed; pistillate inflorescence apparently emersed; peduncle more than 8 cm long, 15 mm in diameter, 3-sided, bracteate; syncarp perhaps a third mature, 9.5 cm long, 6 cm in diameter, ellipsoid, 3-sided, bearing about 1,440 drupes, these 17–19 mm long, 5–6 mm wide, 3–4 thick, the body 12–13 mm long, arcuate spatulate, upper $\frac{1}{3}$ free, cuneate to the base; the pileus 7–8 mm long, the base subsemiorbicular, minutely papillose; the style 4–6 mm long, hornlike, mostly gently curved proximally, the apical ones unbranched, of the

median and lower ones about half are entire with a single horn but the other half are bifurcate and the 0.5–2 mm lobes often are wide-spreading; stigma 3.5–5 mm long; endocarp (immature) oblanceoloid, nearly as long as the body; mesocarp fibrous and fleshy.

HOLOTYPE: Malaya, "Selangor, in the Labu River, forming dense thickets," May 1891, *H. N. Ridley*, (SING). Holotype examined!

Pandanus johorensis Martelli, Soc. Bot. Ital., Bul. 302, 1904; *P. muarensis* Ridl., Mater. Fl. Malay Penin. 2: 226–227, 1907, and Fl. Malay Penin. 5: 77, 1925; (sect. *Rykia*)

Figs. 189, 190

NOM. VERN.: "rassau."

DIAGNOSIS OF ISOTYPE: Leaves 1.3–1.45 m long, 4.2 cm wide, coriaceous, paler beneath, 1-ribbed, 2-pleated, at midsection with 43 secondary parallel veins in each half, no visible cross veins, ligulate, gradually tapering to a 27 cm subulate deltoid apex, this 10 cm down 0.7 mm wide, the base amplexicaul, unarmed, but beginning at 10–11 cm on one side, and at 18 cm on the other the margins with prickles 1.5–2 mm long, 4–11 mm apart, subulate, ascending, dark reddish; the midrib below beginning at 8 cm with prickles 3–3.5 mm long, 12–22 mm apart, stout subulate, arcuate, reflexed; at midsection the margins with prickles 1–1.5 mm long, 4–14 mm apart, stout subulate, arcuate, closely ascending; the midrib below with prickles 1.5–1.8 mm long, 5–45 mm apart, stout subulate, arcuate, reflexed or ascending; on the subulate apex the margins with serrae 0.5 mm long, 1–3 mm apart; those of the midrib below similar but 3–7 mm apart; peduncle 29 mm long, 8 mm in diameter, 3-sided, slightly sinuous, leafy bracted; syncarp single, 6 cm long, 3 cm in diameter, narrowly ellipsoid (very young), bearing about 4,096 drupes, these (immature) 11–12 mm long, 1.5–2.5 mm wide and thick, 5–6 angled, upper $\frac{2}{3}$ free, the body 4.5–5 mm long, oblong-ellipsoid, papillose, with thick longitudinal fibers; style 7 mm long, setiform, hard, shining and yellow; stigma linear, proximal, brown, as long as the style; endocarp and seed not yet formed, but inside the ovary wall

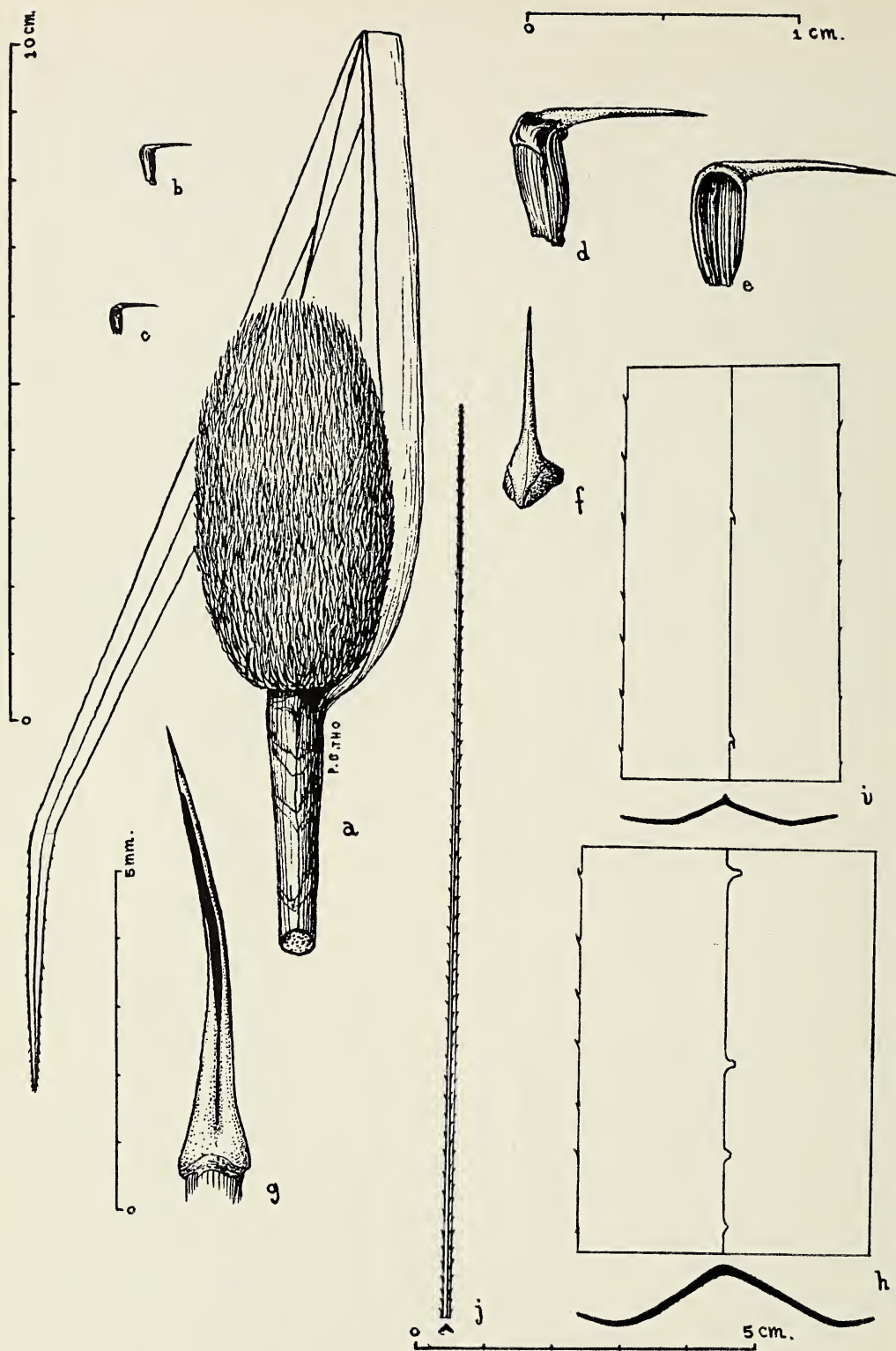


FIG. 189. *Pandanus johorensis* Martelli, from isotype. *a*, Syncarp, $\times 1$; *b*, *c*, drupe, lateral view, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe apex and style, apical view, $\times 4$; *g*, style and stigma, proximal view, $\times 10$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$.

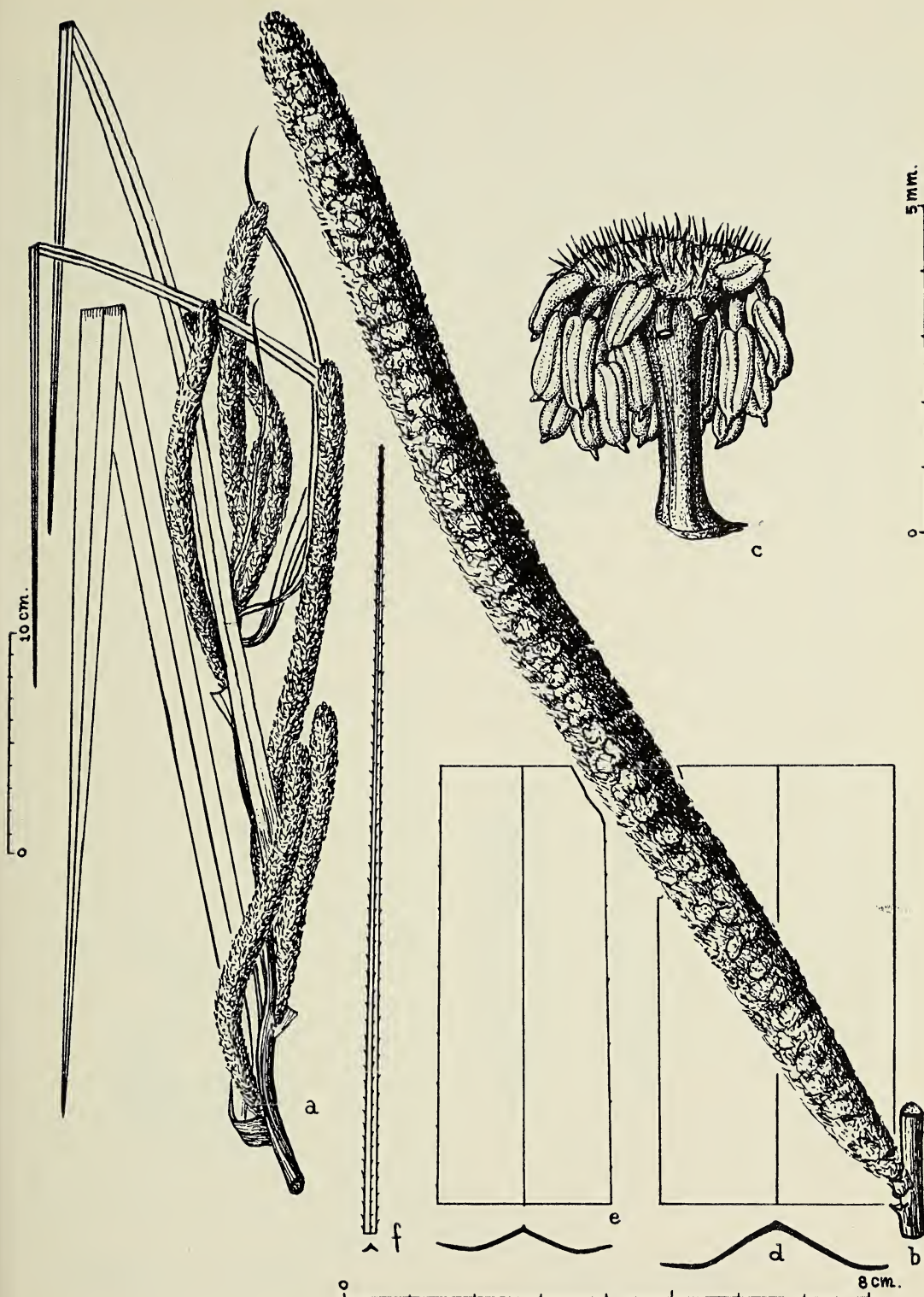


FIG. 190. *Pandanus johorensis* Martelli, from Corner 28,161. *a*, Staminate inflorescence, $\times \frac{1}{3}$; *b*, spike, $\times 1$; *c*, staminate column, scale, and stamens, $\times 10$; *d*, leaf base, lower side, $\times 1$; *e*, leaf middle, lower side, $\times 1$; *f*, leaf apex, lower side, $\times 1$.

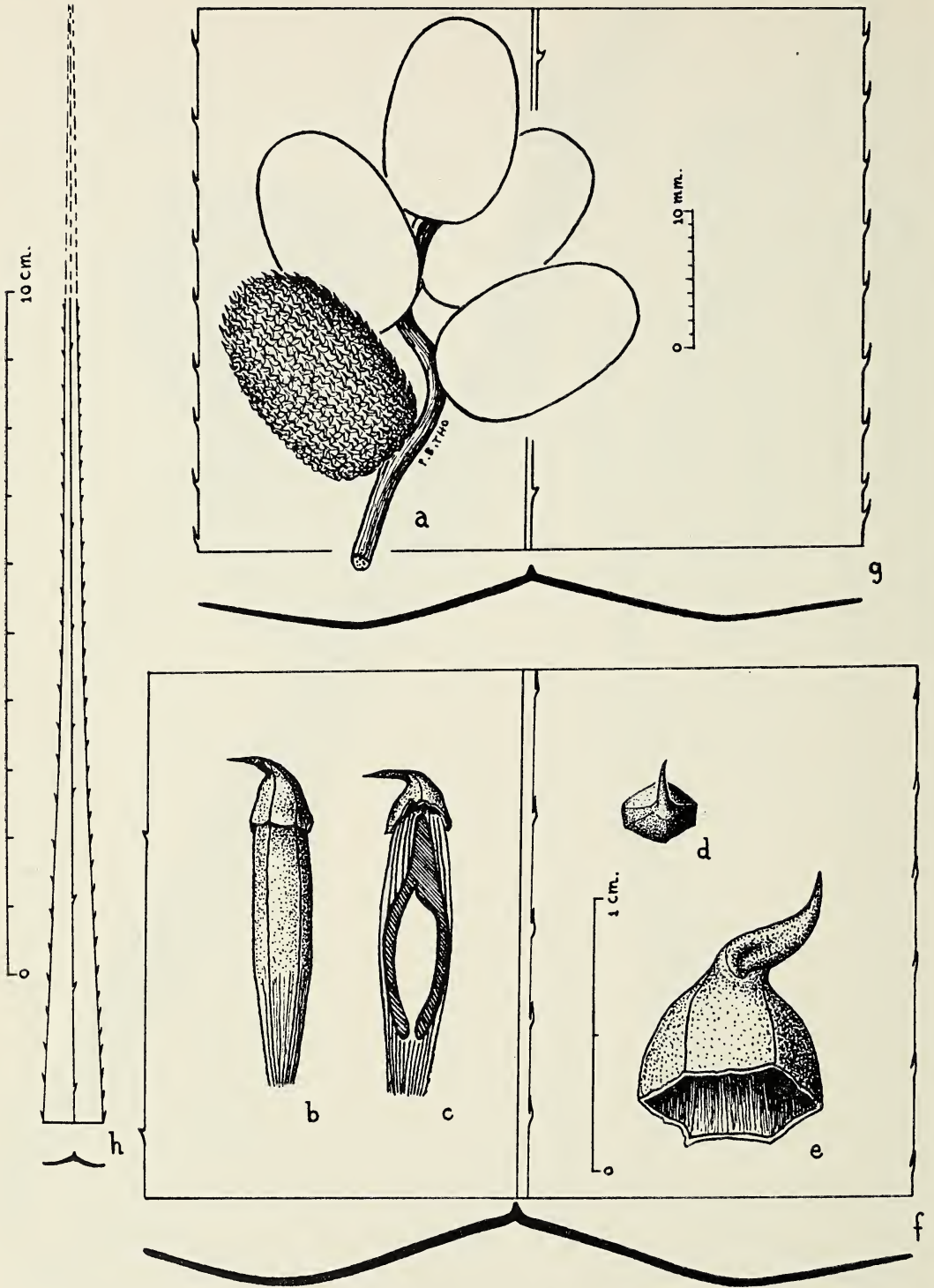


FIG. 191. *Pandanus penangensis* Ridl., from holotype. *a*, Infructescence, $\times 1/5$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe apex and style, $\times 1$; *e*, drupe apex and stigma, proximal view, $\times 4$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$; *h*, leaf apex, lower side, $\times 1$.

of tissue and heavy longitudinal fibers there is a single large cavity, with indefinite traces of inner tissue.

EXPANDED DESCRIPTION FROM ALL PISTILLATE PLANTS EXAMINED: Shrub, to 6 m tall, upper branches 3–4 cm in diameter, dark brown, forming dense thickets, with a few thornlike axillary rootlets 4–6 mm long, divergent; leaves 1–1.8 m long, 2.9–4.1 cm wide; syncarp solitary, pendulous, 12–16 cm long, 6–10 cm in diameter, ellipsoid.

DESCRIPTION OF STAMINATE PLANTS: Bracteal leaves up to 80 cm long, 3.5 cm wide, coriaceous, apparently pale, ligulate, the upper $\frac{1}{3}$ long tapering to a trigonous subulate apex, this 10 cm down 2 mm wide, the lower $\frac{1}{3}$ wholly unarmed, at midsection with 51 secondary veins in each half, no visible tertiary veins; near the apex the margins and midrib below with subulate serrulations 0.5–0.7 mm long, 2–6 mm apart; staminate inflorescence 45 cm long, with 8 spikes, these 15–25 cm long, 12–15 mm in diameter, densely flowered but somewhat interrupted; flowers sweet and sickly scented; filament column 4 mm long, stout, clavate, bearing an apical parasol-like scale 3–5 mm in diameter, the apex hispidulous with hairs 0.3–0.4 mm long; free filament tips 0.5–2 mm long, pendent from the lower surface, glabrous or sparsely hispidulous; anthers 10–16, and 0.8–1.3 mm long, mostly cylindric, bearing an apical mucro 0.2 mm long, formed of a projection of the connective (description from *Corner* 28,161).

ISOTYPE: Malaya, Johor, Muar, Bukit Wiligu, Sungei Pauh, 1902, *Fox* 11,326 (SING). Isotype examined!

SPECIMENS EXAMINED: Malaya, Johore, Mawai, generally flowering of staminate and pistillate on riverside, flowers visited by bees and beetles, May 13, 1934, *E. J. H. Corner* 28,161 (SING).

DISTRIBUTION: Malaya and Sumatra, forming dense thickets in estuaries, forming a zone beginning where *Nipa* stops, in tidal fresh water. Plants with similar leaves have been seen from Borneo.

DISCUSSION: *P. johorensis* Martelli is a member of the section *Rykia*. It was briefly published in 1904 by Martelli as only a few phrases in a key to certain species. His holotype was:

"Stato di Johor. Penis. Malese, no. 11326 Ridl. (H. Becc.)." The specimen above cited is an isotype in the herbarium in Singapore. It bears the data: "Malay Peninsula, Johor, Bukit Wilgu, Sungei Pau, 1902, *Fox* 11,326." In his Materials for a Flora of the Malayan Peninsula 2: 226, 1907, Ridley accepted Martelli's species, and cited the single collection, "Muar: Bukit Wilgu, Sungei Pauh (W. Fox) 11326." Later, Ridley in his Flora of the Malay Peninsula 5: 77, 1925, treated this plant as *P. johorensis* sensu Ridl., not of Martelli, and redescribed it as the new species *P. muarensis* Ridl. For this he had the holotype: "Muar, Sungei Pauh (Fox)." Whatever misconception Ridley thought there was, he had no right to rename the species using the same holotype. Certainly the collection *Fox* 11326 from Bukit Wilgu, Sungei Pauh, Johor, is the same as [*Ridley*] 11,326 with the same locality data. The number is a Singapore Herbarium number, as the staff members were required to use this single series of numbers, not their own personal collection numbers. The holotypic specimen in the herbarium at Firenze was not a duplicate distributed from Singapore. Rather, it is a fragment consisting of about two score of the drupes placed in a paper pocket on which in Martelli's hand is written the data. These fragments were taken from the syncarp of the isotypic specimen, then in Calcutta, now in Firenze. It lacks stem, leaves, inflorescence, and syncarp. Nevertheless, the actual holotype is this fragmentary specimen, *Fox* (or *Ridley*), once in Calcutta, and now in Firenze. However, there seems no doubt but that *P. muarensis* Ridl. is a typonym and must be placed in the synonymy of *P. johorensis* Martelli. The isotype in Singapore has a syncarp with immature drupes that have not matured their endocarp and seed.

Pandanus penangensis Ridl., *Asiat. Soc., Straits Branch, Jour.* 41: 50, (1904) = 1903; *Fl. Malay Penin.* 5: 81, 1925; (sect. *Rykia*)

Fig. 191

DIAGNOSIS OF HOLOTYPE: "Tree 7 m. tall, 10 cm. in diameter"; leaves 2 m or more long, near the base 12 cm wide, when young marbled light and dark green, beginning at 15–16 cm

the margins with prickles 1.3–1.5 mm long, 4–7 mm apart, pale, subulate, flat appressed ascending; the midrib below sharp salient and with similar ascending prickles, the secondary parallel veins conspicuous and in lower part 69 in each half, and except at base the tertiary cross veins prominent on both sides, transverse or oblique and forming short, rather oblong meshes, mid-section not seen; at 45 cm down from the apex the blade 11.5 cm wide, the apex abruptly narrowed to a subulate tip about 5(?) cm long, the margins with subulate serrae 1.5–2.5 cm long, 3–10 mm apart; the midrib below with serrae 0.8–1 mm long, 7–20 mm apart; drupes 42–47 mm long, 7–9 mm wide, 6–7 mm thick, 5–6-angled, the sides smooth, gently curved, probably only the pileus free, the body 37–40 mm long, drupes and pilei shedding separately; pileus 9–11 mm long (or if measured along the curve of the style 13–16 mm long), 10–13 mm wide, 8–10 mm thick, 6-angled, broad ovoid-pyramidal, the tip proximally curved; style 5–7 mm long, heavy subulate, curved

proximally almost to a right angle; stigma 4–5 mm long, lanceoloid, papillose, brown; endocarp 32–33 mm long, narrow ellipsoid, bony, ebony-colored, the inner surface shining, the lateral wall 1–1.5 mm thick; seed 15–17 mm long, 4–6 mm in diameter, ellipsoid; apical and basal mesocarp fibrous and fleshy.

EXPANDED DESCRIPTION FROM ALL SPECIMENS EXAMINED: Leaves to 4 m long, the mid-section 10 cm wide, the margin with prickles 2.8–3 mm long, 5–14 mm apart, stout, heavy based, arcuate subulate, appressed ascending, brown; pistillate inflorescence of 4–5 syncarps, each with numerous drupes; syncarps 15–20 cm long, 9.5–10 cm in diameter, ellipsoid.

HOLOTYPE: "Malaya, Penang Hill from base to the top, in woods." The specimen is labeled: Malaya, Pulau Penang, Fort Hill, 1900, *H. N. Ridley* (SING). Holotype examined!

SPECIMENS EXAMINED: Malaya, Pulau Penang, Government Hill, common on the hill top, but not often in fruit, 29 July 1907, *I. H. Burkill* 2,666 (SING).

Lord Howe Island, A Riddle of the Pacific, Part III

S. J. PARAMONOV¹

IN THIS FINAL PART (for parts I and II see *Pacif. Sci.* 12 (1):82-91, 14 (1): 75-85) the author is dealing mainly with a review of the insects and with general conclusions.

INSECTA

Our knowledge of the insects of Lord Howe Island is only preliminary and incomplete. Some groups, for example butterflies and beetles, are more or less sufficiently studied, other groups very poorly.

Descriptions of new endemic species and records of the insects of the island are dispersed in many articles, and a summary of our knowledge in this regard is lacking. However, a high endemism of the fauna is evident. Although the degree of endemism is only at the specific, or at most the generic level, the connection with other faunas is very significant.

Olliff (1889) wrote an interesting review of Coleoptera of the island. In his time about 80 species of Coleoptera were recorded, but among them were 46 new species and 5 doubtfully new. That is, more than 56% were endemic species. Similar reviews for other groups are lacking.

An interesting large, wingless phasmid with a body length of 106 mm, *Dryococelus* (formerly *Carabidion*) *australis* Montr., is now probably extinct. Gurney (1947: 391) wrote: "The present status of *Dryococelus* is uncertain. A note in Ward's Natural Science Bulletin (vol. 8, No. 2, p. 11, 1935) indicated that the species is extinct, but I have been informed by John W. H. Rehn, of the Academy of Sciences of Philadelphia, that he has seen a recently published note suggesting that the species is maintaining itself."

During two visits to the island, in 1954 and 1955, the author failed to find the insect. An official enquiry was made recently to the Administration staff of the island, and the author received a letter from the Superintendent of the Island, Mr. H. Ward, on Nov. 3, 1961, in which he states: "A number of the old inhabitants have been questioned and all have advised that it is at least 30 years and possibly 40 years since this insect has been seen on the Island. A member of the staff, aged 33 years, has never seen or heard of the insect, nor has any pupil of the local School."

The only possibility is that the insect may still exist in one of the biggest banyan trees on the slope of Mt. Gower, on the lagoon side. The area is well isolated from the settlement where the rat concentration was probably the greatest, and may have survived in crevices of the tree.

The presence of the insect in the past is evidence of an ancient connection with Australia or some other continent by a land bridge; any other type of transportation is highly improbable.

A very interesting example of distribution is found in an archaic Homopterous family, the Pelorididae, with very limited possibilities of movement (nearly wingless), and adapted to very restricted habitat. There are 15 species recorded now for the whole world. Thirteen of them are associated in Chile, New Zealand, Tasmania, and eastern Australia with the southern beech *Nothofagus*. The plant also grows in New Caledonia, and Dr. J. W. Evans (Director of the Australian Museum) visited this island especially to search for Pelorididae. None were found, nor was an environment discovered which would be favourable for their existence.

In 1959 J. W. Evans, having been informed that a single nymph was recorded from Lord Howe Island, visited the summit of Mt. Gower

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Manuscript received February 27, 1962.



FIG. 1. A typical cloud "carpet" covering the summit of Mt. Gower while the rest of the island is in sunshine. This "carpet" preserves the humidity and coolness over long periods, in strong contrast with other parts of the island. (Photo by Miss Z. Liepa.)

and during 3 hr (*sic*) found two new species of this family.

It is interesting to note that *Nothofagus* is absent from Lord Howe Island, but 24 adults and 7 nymphs of Pelorididae were found in moss. Probably the Pelorididae are not especially associated with *Nothofagus*, but require, above all, high humidity with cool temperatures. It is evident that this family has lived on the island in a very specialised habitat for millions of years. The possibility of transportation must be excluded. It means that the general conditions for life are unchanged: the summit of Mt. Gower is a refuge for species ecologically close to recent New Zealand fauna and flora (see Fig. 1), whereas at sea level are preserved elements from the north, from purely tropical areas.

It is noteworthy that, of the endemic palms, two dwarf species grow not at sea level, as do

two others (see Fig. 2), but much higher up, closer to the summits of the two large mountains.

The submerged land "Howeania" was isolated from Australia, or connected only in the far north, and the present "Australian" elements we must regard as casual elements, not as having come by a direct land bridge. The Australian elements play an important role in the composition of the flora and fauna of the island, but it is remarkable that the most typical Australian forms, the Australian "*sui generis*," are absent.

The Diptera of the island have not been reviewed, the main obstacle being the lack of knowledge of the fauna of surrounding areas. The dipterofauna in general is very impoverished, because the island lacks fresh water basins, and the running streams are of temporary character. Therefore the families and

genera connected in their life history with water are absent. Sandy ecological niches are also poorly represented, and in general the ecological uniformity is a factor which limits the richness in flies.

However, many new species were discovered from the families Asilidae, Muscidae, Ortaliidae, Leptidae, Calliphoridae, Tachinidae, etc. (see references).

The author has the impression, however, that most of the endemic species are represented in the surrounding areas by closely related species. Nothing extremely old or "extra" was found; however, only the lower part of the island has been comparatively studied. The middle zone (about 1,000 ft) and the high zone (2,000 ft and above) are practically untouched. The small fresh-water streams and pools deserve the special attention of collectors.

The author observed the hatching of enormous numbers of *Lucilia* and *Sarcophaga* from

the sand on the beach. They emerged early in the morning, and with wings still undeveloped walked onto the small rocks on the shore, the surface of some of the rocks being absolutely covered with them. Here they waited until their wings were developed and then flew away. The sandy area is covered by sea during high tide, but the puparia apparently are not harmed. The author observed no hatching from the sandy areas not reached by the high tide.

To illustrate the state of our knowledge of the Lord Howe Island fauna we may quote the results of J. D. Bradley's collecting in 1953: in 1½ days of collecting, among 22 specimens of Microlepidoptera there were 12 species, 8 of which were new, and 4 others which were Australian species not previously recorded for the island.

The island is also very suitable for experiments in insect biological control. In October



FIG. 2. Two endemic species of palms which dominate the lower part of the island. Before the last war the export of their seeds was an important industry of the island. (Photo by Miss Z. Liepa.)



FIG. 3. An "Arcade" on Admiralty Island. The greyish dots in the air are sea birds which nest there. The basalts form the main mass of the island. (Photo by Miss Z. Liepa.)

1959, specimens of *Opius oophilus* were liberated there to control the Queensland fruit fly, *Strumeta tryoni*, and the parasite was recovered in March 1961. The small size of the island greatly facilitated the experiments.

It is impossible to go into details about the insect fauna of the island as the available data are too fragmentary. However, some points are very significant, especially those concerning wingless insects (and birds); they show a close relationship to the New Zealand fauna and to the eastward land masses in general. The Australian element, considered numerically, may be larger than that of New Zealand or Polynesia, but the proximity of the Australian continent, its great extension northwards and southwards, and the direction of the prevailing winds in the southwest Pacific no doubt account for this preponderance. If we take as an example the plant genera which are confined to Australia and Lord Howe Island (*Notelaea*,

Melaleuca, *Lyonsia*, *Lagunaria*, and *Westringia*), we must not overestimate the importance of this fact, because the most characteristic Australian genera are either entirely absent from Lord Howe Island or represented by only one or two species. This means that these species have had more facilities for transportation, natural or by man.

Summarizing all the data in our hands, we can say from its fauna that Lord Howe Island is not a part of the Australian zoogeographical region, but is closer to the New Zealand sub-region.

GEOLOGY

In order to understand the history of the fauna and flora the geology also must be considered. The general geology of the island is very simple; the island consists mainly of two principal formations: the volcanic rock which

forms the general mass (see Fig. 3), and the stratified beds resting on it (see Fig. 4). Two thirds of the island is composed of volcanic rocks, comprising three isolated masses.

Edgeworth (1889: 132) summarized his study of rocks as follows:

1. All the igneous rocks of Lord Howe Island (so far as represented by the collection examined) belong to the Basalt group.
2. A vast period of time must have elapsed between the eruption of the diabasic basalt and that of comparatively recent olivine basalt.
3. All the basalts, with the exception of the diabasic types, are probably not earlier than Tertiary, and some may be Post-Tertiary.
4. The diabasic basalt is probably Pre-Tertiary, or may be Paleozoic.

Immediately overlaying the volcanic rocks, and between them and the succeeding coral-sand rock series, occurs a bed of stiff unctuous red or yellow clay. It does not appear to be fossiliferous.

More interesting is the coral-sand rock series; this deposit is often from 30 to 40 ft high. The coral-sand rock is the chief fossiliferous deposit of the island, and has yielded the remains of the interesting reptile *Meiolania*, eggs of turtles, bird-bones, and recent species of both land and marine shells.

A systematic boring of this deposit, as well as of coral beds in the sea, may give us a detailed picture of the island's physical history. Unfortunately, geological study is only at a preliminary stage, and when it was stated that no minerals of economic value existed on the island further investigations were stopped.

The island deserves, however, our special attention as a very convenient object where the history of Australia, of the surrounding areas to the east, and of the Pacific may be studied much more easily than at other points.

The impoverished fauna and flora and the simple geological structure may give us all



FIG. 4. A typical stratified deposit at the eastern seashore east of Old Gulch; the coral-sand strata are prominent. (Photo by Miss Z. Liepa.)

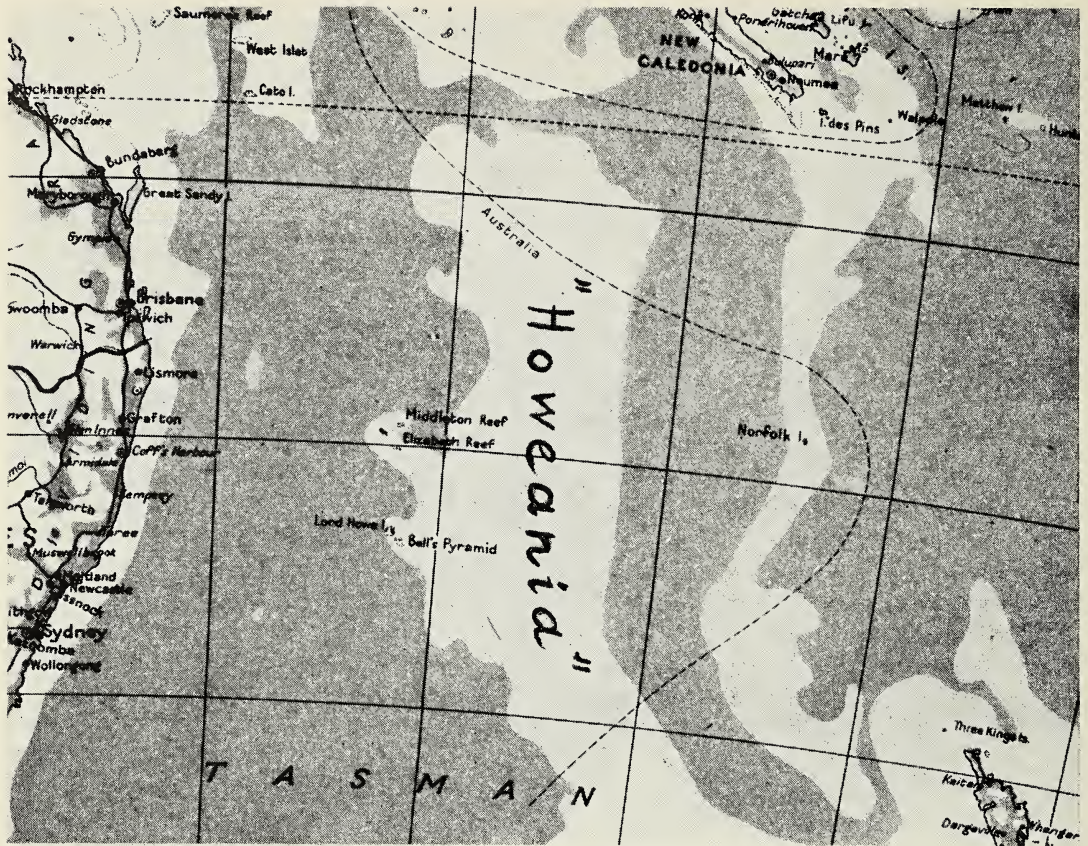


FIG. 5. Map showing the area of "Howeania."

the necessary data, because of the small volume of material for study. Lord Howe Island may be the focal point for the study of this area of the Pacific.

An enormous number of facts about the Australian continent remain to be studied, and this will require many years of work, but the general outline of the history of organisms and environment may be elucidated much more rapidly if we know the history of Lord Howe Island. For developing synthetic conclusions the island represents an extremely useful area.

COMPOSITION OF THE FAUNA AND FLORA

The fauna and flora of the island probably consists of three different layers of animals and plants:

1. The remnant from the very large land mass, now submerged, which we have called "Howeania." This remnant is the oldest part of the fauna and flora.

2. Immigrants from surrounding areas, arriving after the land was submerged, i. e., very long ago, in the geological sense. These elements have had time to develop into new species.

3. Recent immigrants, helped directly or indirectly by man. We have some data which indicate that in recent time several species arrived on the island, but finding conditions unsuitable for permanent settlement they disappeared.

The history of the fauna can be illustrated with the help of Figure 5. If we suppose that the shallow area of the sea, shown by the white area, was the outline of the submerged land

(Howeania), then the peculiarities of the fauna and flora of the island can be explained easily.

The absence of typical Australian elements was caused by the very wide and deep part of the sea in between, which acted as an impassable barrier.

The presence of Australian elements which are not typical for the Australian fauna can be explained by the very narrow strait in the north (see dotted line of Tropic). It permitted the penetration of tropical elements, whilst the elements more adapted to moderate climate could reach the island from the south, where there was a broad land connection with New Zealand.

The very essential difference between the faunas of Lord Howe and Norfolk Island may be explained by the very large and deep sea area extending eastwards from Howeania. Since it is about halfway between New Caledonia and New Zealand and was connected to them by land, Norfolk Island contains elements of both countries.

The New Zealand elements are not represented so well on Lord Howe Island because the ecological conditions are very limited spatially, and they are confined mostly to the mountain summits of the island.

We have reached all these conclusions after attentive study of the animals and plants, details of which can not be demonstrated in a work of this size. The author reached these conclusions before consultation of the above map showed the distribution of the deep and the shallow portions of the sea. The illustrated structure of the sea bottom fully supports the author's considerations, which are not purely theoretical speculations based on the study of biology, but reflect also the history of the land masses in the discussed area. Here we have a working theory for reconstruction of the history of the island and its life. The theory also explains satisfactorily the history of the basic part of the island's fauna.

With regard to the immigrants which reached the island after the submergence of Howeania, the position is less satisfactory: first, there is a lack of data about the fauna of the island; second, data are lacking about the distribution of organisms in the surrounding areas.

Without these data, reconstruction of the history of the fauna and flora is impossible.

Regarding comparatively recent immigrants, we must consider the role of man in the distribution of plants and animals. Early whalers must have played a considerable part. If, for example, we find on the island a plant which has a strange, widely interrupted distribution, such as South Africa and the island, and grows near the sea shores, we have grounds to suspect that the plant has been transported by ships. As an example, we may cite the case of the so-called "African water lily" in Australia (*Aponogeton distachyum*, or Cape Pond Lily). The author found the lily in 1947 in the lagoon at Lorne, Victoria. This plant is very abundant there, and in July the entire lagoon is covered with the white flowers. The lily is rapidly diminishing in numbers, however, and we must predict that sooner or later it will disappear from the lagoon.

During the last century whalers introduced many animals and plants along the sea shores which they visited. One of the island's chief industries began in this fashion, i. e., the culture of the high quality onion, some bulbs of which had been washed ashore, found by an island woman, and planted.

COMPOSITION OF THE FLORA

Oliver (1917) gave an analysis of the composition of the island's flora. Although the data are outdated in nomenclature, the conclusions may be regarded as valid.

Of the 169 genera of vascular plants represented on Lord Howe Island 4 are endemic. Of these 4 genera, *Colmeiroa* and *Hedyscepe* are allied to New Zealand forms, *Negria* to both New Zealand and New Caledonian genera, and *Howea* to Malayan and tropical Australian genera.

If the five species belonging to these 4 genera be taken as modified descendants of species which arrived via a land bridge, then they would indicate a New Caledonia-New Zealand migration, with the land connection severed first at the southern end, thus accounting for a greater degree of peculiarity for the species related to New Zealand forms.

Of the nonendemic genera 95 are widely distributed, occurring in New Zealand, Australia, and Polynesia; 47 others range widely through tropical countries, but do not reach New Zealand; 1 occurs in New Zealand only; 5 in Australia only; 3 in Polynesia only; 11 in New Zealand and Australia only; 2 in New Zealand and Polynesia only; 1 in Africa only.

It is interesting to state, and Oliver omitted to do so, that most of the genera are represented only by a few species: 169 genera are represented by 209 species, which means that speciation is not strong on the island. Progressive evolution was almost absent on the island, and we have only transformation, probably due to genetic impoverishment in the populations.

It is possible also that some endemics of the

island are only relics of species more widely distributed in the past, and now preserved only on the island.

If we compare the number of the very widely distributed genera (see above) and the genera with very restricted areas, we see a great difference: of 165 nonendemic genera 95 are distributed in New Zealand, Australia, and Polynesia; 47 only in Australia and Polynesia; and only 23 belong to the different countries, but are isolated.

The presence of a large portion of widely distributed genera and species might have been expected in the flora of an isolated island, because species possessing facilities for wide dispersal would naturally form the bulk of immigrants after the land connection had been severed.



FIG. 6. View of the lagoon from the south; in the background are Rabbit Island and Mt. Eliza; on the seashore are three *Araucarias* introduced from Norfolk Island, growing well among the native plants. Taken at low tide. (Photo by Miss Z. Liepa.)



FIG. 7. The lagoon viewed from the south during low tide. In the foreground are coral reefs, of interest to the marine zoologist; behind these is low Rabbit Island, and in the background is the northern part of the island with tooth-shaped Mt. Eliza. (Photo by Miss Z. Liepa.)

This means that we must be very careful in making conclusions based only on numerical data. For the history of the flora and fauna the easily distributed elements are practically valueless.

Let us turn to the analysis of the species. Of 209 species of the flora 70 (or 33%) are endemic. The percentage of specific endemism is

very high. Oliver gives the following table which is very instructive:

From Table 1 (from Oliver, 1917) it is evident that endemic forms of Lord Howe Island are distinctly more closely related to New Zealand and Polynesia than to Australia. As a result, the line of Gressitt (1956) must be transferred westwards of Lord Howe Island, separating it from the Australian continent. The zoological data also have shown that the fauna of the island is more closely related to the lands to the east than to Australia.

A direct connection of Lord Howe Island with Norfolk Island, however, is doubtful, because the *Araucarias* of Norfolk Island have not reached Lord Howe Island naturally, although those transplanted by man are growing very well (see Fig. 6).

TABLE 1

	TOTAL NO. OF SPECIES	ENDEMIC SPECIES INCLUDED IN TOTAL	PERCENTAGE OF ENDEMIC FORMS
Whole flora	209	70	33
Australia	168	41	24
New Zealand	109	38	35
Polynesia	116	39	34



CONCLUSIONS

1. Lord Howe Island is not an "oceanic" island owing its existence to the activity of corals, although some part was played by them; the island's fauna and flora are not a casual "mixtum compositum" of elements arrived by various methods from different directions, during different epochs.

2. Lord Howe Island is a small part of a sunken continent or large island, preserving a very specific fauna and flora, with very high endemism (in some groups as high as 70%).

3. Some endemic species developed here probably as a result of very long isolation from the closely related population in the surrounding areas; other endemic species (some birds) probably are unchanged species preserved from the sunken land, being mostly destroyed by man in the surrounding areas.

4. The sunken land ("Howeania") was never connected with the Australian continent after creation of Eucalyptus and Acacia species, because on the island they are absent, although

growing very well when introduced. It appears that the island's isolation is very old.

5. Lord Howe Island was probably never directly connected with Norfolk Island. The Araucarias of Norfolk Island, so typical of that island, are absent from Lord Howe Island. The species common to both islands are probably species with very strong capacity for dissemination.

6. Having no land connection with Australia and Norfolk Island, Lord Howe Island received its fauna and flora mostly from the north and south. Warmth-loving elements of the flora and fauna probably arrived from the northeast (palms, for example). All the tropical elements show a connection with this direction.

7. The elements of subtropical or moderate areas, liking cool climate and high humidity, probably arrived from southeastern and southern directions (the so-called New Zealand elements have their origin in these sectors).

8. Since it is a highly elevated island (up to 2,800 ft) Lord Howe Island has preserved its character, and its flora and fauna, for a long period of geological time. The flora and fauna of its summits (for example the plant *Dixonia*

FIG. 8.

1. Mt. Eliza
2. Caves in this area
3. North Hills
4. Dawson Peak
5. Poole's Lookout
6. North Ridge
7. Grassy Hill
8. North Scab
9. Old Settlement Creek
10. Thomson's Lookout
11. Settlement Creek
12. Hine's Curio Shop
13. "Ocean View" Guest House
14. The Peg
15. "Somerset" Guest House
16. Thomson's General Store

17. Electric Power Station
18. "Waverley's" Tea Rooms
19. "Dignam's" Tea Rooms
20. The Hall
21. "Leanda Lei" Hotel
22. Doctor
23. Post Office & Bank Agency
24. Hospital
25. Government House
26. School
27. "Pine Trees" Guest House
28. Nichol's Clear Place
29. Blinky Beach Picnic Hut
30. Lagoon
31. Soldier's or Big Creek
32. "Smoking Tree"
33. "Goat House"

Asterisks indicate localities known by more than one name. Those currently used on the island are shown on the map and alternative names are listed below:

Admiralty Islets: Roach Islets
Blinkenthorpe Bay: Ross Bay
Lion Point: Mutton Bird Point
Mt. Malabar: North Peak
North Bay: Callam's Bay
North Rock: North Islet

Old Gulch: Collin's Cove
Rabbit Island: Blackburn or Goat Island
Rabbit Island Passage: Boat Passage
South Entrance: Erscott's Passage
Sugarloaf: Soldier's Cap
Transit Hill: Lookout Mountain

antarctica, and the Pelorididae insects) are very old elements, preserved in a nearly unchanged condition for many millions of years. It is evident that after the ancient land sank, there was no re-elevation of it which deserves serious attention (there were only slight oscillations of ocean).

9. At the present stage of our knowledge of the geology, paleontology, and biology of the island, it is impossible to draw any conclusions concerning the theory of drifting continents: there are no positive and no negative data.

10. Finding of interesting data can be expected after a study of Ball's Pyramid. This colossal rock has never been touched by exploration, and no specimens either of plants or of animals have been collected there. The possibility is not excluded that some forms which have been destroyed on the island may have survived on this rock.

11. There are numerous caves on the island, some very long, which have not been explored; we have reason to think that interesting remains of recent and past fauna may be preserved there.

12. The presence of a coral reef gives an opportunity to gather additional data about oscillations of the sea level, and their magnitude (see Fig. 7).

13. The preliminary data at our disposal give evidence that in the past there existed a large land mass, probably southeastward from Lord Howe Island, where the flora and fauna of the island developed. On the island itself we can find only remnants of this life of the past.

14. Lord Howe Island is a particularly interesting subject for the study of the Pacific and surrounding countries. The scientific value of the island has been underestimated, almost neglected. Only one expedition, organised by the Australian Museum in 1887, has worked on the island. Since then any study that has been done has been private, and by amateurs.

This article shows that the island deserves more serious attention: its interest is not local but international. Only longer expeditions of geologists and biologists, working together, can supply us with the necessary data.

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NOTES

Additional Plants from the Midway Islands

A collection of plants from the Midway Islands, made by Dr. Hubert W. Frings, Department of Zoology, University of Hawaii, on April 16, 1962, includes four species not previously recorded from there. These are:

GRAMINEAE

Polypogon monspeliensis (L.) Desf.,
Eastern Island.

CRUCIFERAE

Coronopus didymus (L.) J. E. Smith,
Eastern Island.

EUPHORBIACEAE

Euphorbia peplus L., Sand Island.

PRIMULACEAE

Anagallis arvensis L., Sand and Eastern
Islands.

All four of these species, although not native to Hawaii, are now found on the major islands of the Hawaiian chain and were probably introduced accidentally to Midway from Oahu. At various times ornamental plants, and the soil in which to grow them, have been taken to Midway from Honolulu. It is likely that seeds of the plants reported here reached Midway in such soil.

Dr. Frings' collection included 27 species of vascular plants, which he described as the more common species on the atoll. It is of interest to note that only 5 of these species (*Boerhavia diffusa* L.; *Tribulus cistoides* L.; *Ipomoea indica* (Burm. f.) Merr.; *I. pes-caprae* (L.) Sw.; *Scaevola sericea* Vahl) are native to Midway. This provides some indication of the changes in the flora, and concomitant changes in the ecosystem, which are related to man's activities on Midway.

This collection has been deposited in the herbarium of the B. P. Bishop Museum in Honolulu—Charles H. Lamoureux, Department of Botany, University of Hawaii, Honolulu, Hawaii.

On Malayan Shores: A Review

S. H. Chuang. 1961. *On Malayan Shores*. Pp. xvi+225; 112 numbered plates and frontispiece (13 plates and frontispiece in color), 28 text figures. 5.5 × 7.5 inches (14 × 19 cm). Published by Muwu Shosa, P. O. Box 1813, Singapore.

It is for this incredibly rich center of the great Indo-West Pacific marine flora and fauna that Dr. Chuang's small volume is intended as an introduction. He did not write the book for the specialist in any one group, or even for the trained marine biologist, but for the "amateur naturalist." With this aim he has avoided as much of the specialized language of zoology as

possible; his descriptions of plants and animals are short and point out only one to several salient characteristics; he uses no keys and gives no synonyms. On the other hand his illustrations are numerous and excellent: some 50 species are illustrated by line drawings in the text figures and over 500 are represented by clear reproductions of photographs in the 112 plates. He has limited himself to the more common and conspicuous species, as would be expected; he does not touch upon the fishes which have been dealt with in previous books.

The book is divided into two parts, the first is a general review of aspects of marine biology

applicable within the scope of the work, the second is a systematic review. The first section includes chapters on the chemistry of sea water, zonation of the shore, coral reefs, plankton, etc. There is also a chapter valuable for a trained biologist visiting the peninsula which discusses Malayan collecting localities (Chapter VI). The second portion is divided among seven phyla, although eight or nine additional phyla are discussed, with species named, in the chapter on animal life of Part I. The appendix gives faunal lists for four typical shore habitats. A glossary gives Malayan names for over 100 species. The bibliography is short and covers only those books cited in the text, not the systematic works from which the nomenclature was derived. The index is very complete, listing all systematic names applied to all taxa, English common names, topics discussed in the first part of the book, and authors cited; it even includes a glossary to some of the more technical terms used, as "siphonoglyph" and "periostracum."

While this book is addressed only to the

amateur, it obviously will be used by two other groups: students of biology in Malaya, and marine biologists visting these waters for the first time. Having spent a year working on the adjacent Gulf of Thailand, and having briefly visited Malayan shores, I can attest how extremely valuable this volume will be to visitors. Moreover, because the fauna from India to Indonesia, from the Coral Sea to the South China Sea is basically the same, it will be of use to all visitors to the Western Pacific and adjacent Indian Ocean.

Admittedly the book has limitations: it is not an exhaustive scientific monograph on the flora and fauna. Yet if it were, it would not be one small volume, but many large volumes. Rather than disparage the book for omissions, we should commend the author for producing a volume of considerable value to biologists, and regret that books such as this are not available for other areas in the tropical Pacific.—*A. H. Banner, Department of Zoology, University of Hawaii, Honolulu, Hawaii.*

Manuscript Form. Manuscripts should be typed on one side of standard-size, white bond paper and double-spaced throughout. Pages should be consecutively numbered in upper right-hand corner. Sheets should not be fastened together in any way, and should be mailed flat. Inserts should be either typed on separate sheets or pasted on proper page, and point of insertion should be clearly indicated.

Original copy and one carbon copy of manuscript should be submitted. The author should retain a carbon copy. Although due care will be taken, the editors cannot be responsible for loss of manuscripts.

Introduction and Summary. It is desirable to state the purpose and scope of the paper in an introductory paragraph and to give a summary of results at the end of the paper.

Dictionary Style. It is recommended that authors follow capitalization, spelling, compounding, abbreviations, etc., given in *Webster's New International Dictionary* (unabridged), second edition; or, if desired, the *Oxford Dictionary*. Abbreviations of titles of publications should, if possible, follow those given in *World List of Scientific Periodicals*.

Footnotes. Footnotes should be used sparingly and never for citing references (see later). When used, footnotes should be consecutively numbered by superior figures throughout the body of the paper. Footnotes should be typed in the body of the manuscript on a line immediately below the citation, and separated from the text by lines running across the page.

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BATZO, RODERICK L., and J. K. RIPKIN. 1849. A Treatise on Pacific Gastropods. Rice and Shipley, Boston. vii + 326 pp., 8 figs., 1 map.

CRAWFORD, DAVID L. 1920a. New or interesting Psyllidae of the Pacific Coast (Homop.). *Proc. Hawaii. Ent. Soc.* 4(1): 12-14.

——— 1920b. The sandalwoods of Hawaii. *Proc. Hawaii. Ent. Soc.* 4(2): 374-375, 13 pls.

In the text, sources should be referred to by author, date, and page, as follows: "It was noted (Rock, 1916: 18) that . . ." or "Rock (1916: 21-24) says . . ."

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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

JEN-HU CHANG

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Gibsmithia hawaiiensis gen. n. et sp. n.

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Part 16. Thailand and Vietnam

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The Role of Climatology in the Hawaiian Sugar-Cane Industry: An Example of Applied Agricultural Climatology in the Tropics¹

JEN-HU CHANG

CLIMATOLOGICAL STUDY in the Hawaiian sugar-cane industry has a long, noteworthy history. Meteorological observations on the plantations were initiated in 1883, preceding the establishment of the first official weather bureau station in Hawaii by fully 20 years. The climatological network in the cane-growing areas expanded by leaps and bounds to 50 stations at the turn of the century, and to 500 stations in 1960 in an area of only 350 sq miles (Fig. 1).

In the late 1920's and early 1930's Das (1928, 1931a, 1931b, 1932) used the rainfall and temperature records to define the effect of climate on crop yield and juice quality in a simple, direct manner. He also advocated the use of day-degree as a guide to irrigation control (Das, 1936). Investigations along the same line of climate-and-plant complex were carried further by Williams (1933), Borden (1940, 1949), Clements (1940), Swezey (1942), and others into the early 1940's.

At the end of World War II meteorologists, freshly relieved from their wartime duties, were able to turn their attention to a multitude of peacetime problems. The Hawaiian sugar industry promptly seized this opportunity. The Experiment Station and the Pineapple Research Institute founded their joint Meteorological Department in 1946 and contracted with a group of meteorologists at the University of Chicago to investigate dynamic and regional climatology of Hawaii. The culminating results of this intensified research were a series of papers in the Meteorological Monographs, discussing the general circulation, weather types, local flow patterns, rainfall statistics, and the like. Such studies inevitably led to the improvement of forecasting and furnished valuable information for operational planning.

At the half-century mark, when weather

modification was a new subject, the industry embarked upon an intensive study of cloud seeding. Leading scientists from seven research institutes in the U.S.A. and abroad participated in the so-called "Project Shower." It was hoped that the Hilo coast, with its humid trade winds, would provide an ideal environment where rainfall could be induced by the addition of chemicals to the warm clouds; it was soon realized, however, that scientific know-how of artificial rainfall was probably still decades away. The project nevertheless produced valuable information in the field of cloud physics.

Realizing the limitations upon man's ability to modify weather on a grand scale, the industry sought instead to improve the efficiency of water use through the study of micrometeorology. In 1957 an evapotranspiration project was initiated at the Experiment Station. Apart from its obvious application in irrigation planning, the determination of potential evapotranspiration provides a vital link for solving the energy budget and water balance equation in the soil-plant system. The solution of these equations renders the climate-and-yield relationship amenable to quantitative treatment.

Climatological study in the Hawaiian sugar industry thus encompasses a wide variety of topics. More than 50 papers have appeared in a dozen scientific journals. The industry ranks among the leaders in the study of agricultural meteorology. The experience gained during the past three decades may very well benefit research workers in other parts of the world, especially those in the tropics. This paper attempts to summarize these studies. It is hoped that such a stock-taking will not only serve as a reminder of our past accomplishments but also as a guidepost for planning future research.

TRADE-WIND WEATHER

The subtropical high pressure cell in the Pacific Ocean with its attendant trade wind is the

¹ Contribution No. 121, Experiment Station, Hawaiian Sugar Planters' Association, Honolulu, Hawaii. Manuscript received June 14, 1962.

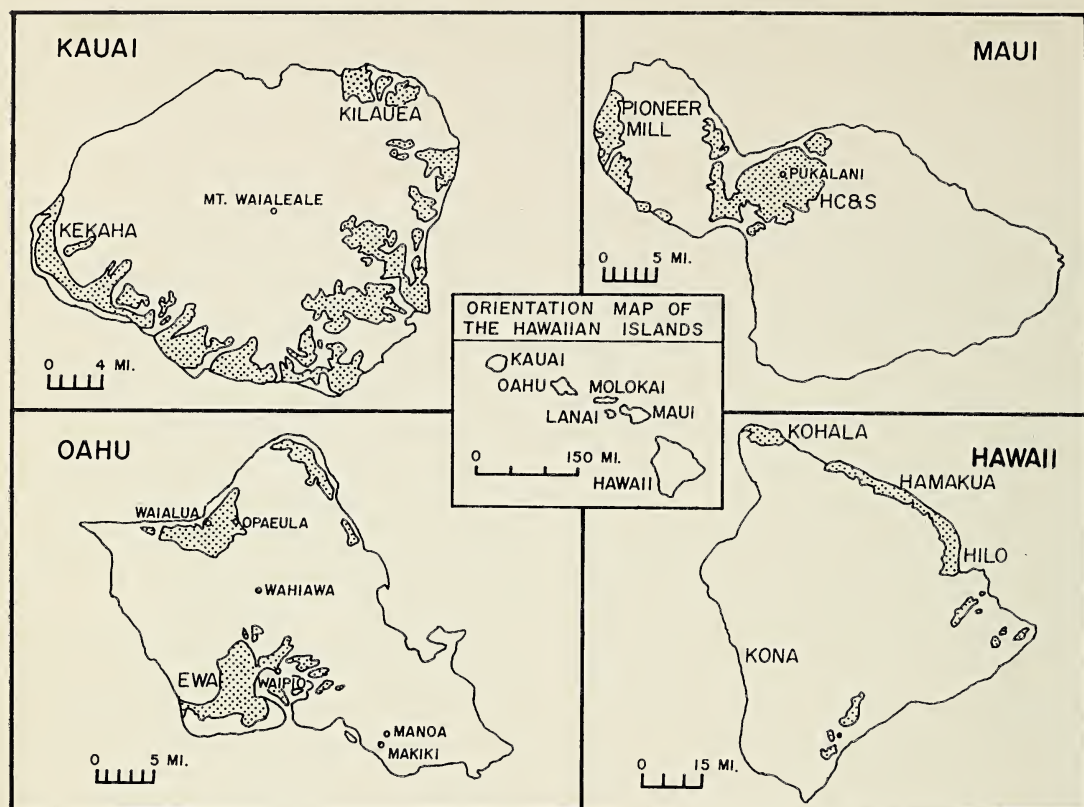


FIG. 1. Location map.

basic circulation in Hawaii; all other weather types are perturbations in this basic current. The eastern portion of a subtropical anticyclone is characterized by divergence and subsidence and consequent adiabatic heating and pronounced dryness aloft. There is, however, a mixing layer near the surface where the air in contact with the cold ocean currents becomes cold and humid. These two layers of air are separated by a zone of temperature inversion which, along the California coast, occurs at an altitude of about 1,500 ft. Downstream, toward the west, as water temperature rises and subsidence weakens, the trade-wind inversion reaches a height of about 6,000 ft in Hawaii.

Figure 2 shows the vertical structure of trade wind in Hawaii. The air below the inversion is moist, with a mixing ratio of 12–15 gm/kg at the ground surface. In the absence of orographic uplift this moist air is a poor rain-producer be-

cause the trade inversion acts as a lid to oppose the development of convective clouds; therefore, in lowland areas, the trade wind is atmospherically moist in terms of humidity but ecologically dry in terms of rainfall.

The air below the trade inversion has a lapse rate close to dry adiabatic. It requires only a little uplifting to produce rainfall. Baer (1956) has demonstrated theoretically that if the relative humidity is approximately constant below the inversion layer, rainfall would increase with height exponentially up to the base of inversion. The logarithmic distribution of rainfall with height is a unique climatic feature in Hawaii.

The prevalence of trade-wind weather in Hawaii is dependent upon the location and strength of the Pacific subtropical anticyclone. In July and August, when the subtropical ridgeline in the high troposphere is located to the north of the islands, the trades prevail during 97% of

the time (Yeh et al., 1951a). In winter, when the subtropical anticyclone moves southward, the frequency of trade-wind weather decreases to 40–50% (Fig. 3).

OTHER WEATHER TYPES

During one-third of the year, when the trades are not prevalent, weather in Hawaii falls into two general types: mixed and cyclonic. The mixed type is characterized by the presence of an essentially east-west polar front north of the islands. This type is a very poor rain-producer as the front is located at a distance. The mixed type often ushers in cyclonic weather.

Cyclonic weather occurs in Hawaii during 22% of the year. The cyclonic weather may be further divided into four subtypes: (1) extratropical cyclones, (2) *kona* storms, (3) easterly waves, and (4) tropical cyclones or hurricanes. The first two subtypes occur most frequently in winter while the latter two subtypes are primarily summer disturbances.

Uncomplicated extratropical cyclones occur only when the zonal westerlies move southward into the tropics. They are, however, weakened on their journey southward and produce only

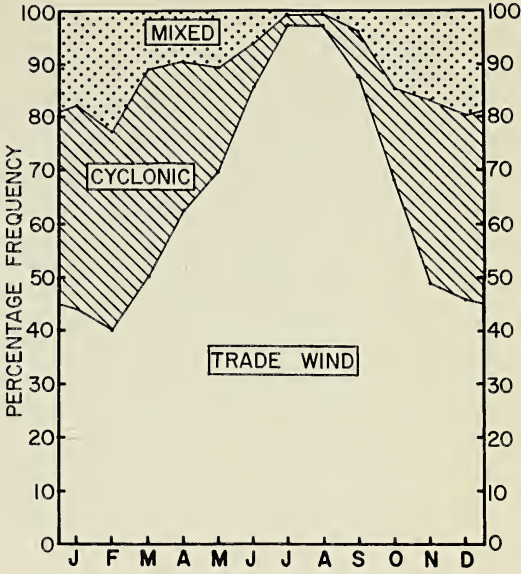


FIG. 3. Monthly variation of frequencies of three weather types.

small rains. Some of these cyclones reach only the northern island of Kauai.

The *kona* storm is essentially a cold-core low developed in the tropics. Simpson (1952) has described two main processes in its formation: (1) the transformation of mid-latitude cyclones which have been trapped at low latitudes by blocking action of a warm high; (2) the cyclogenesis in the easterlies triggered by the building down of a pre-existing cold upper low usually at the southern extremity of a polar trough. Once formed, all *kona* storms seem to assume the same characteristics. The term *kona* indicates that the wind during such a synoptic period is southerly. *Kona* storms occur about three or four times a year, bringing heavy rainfall throughout the islands. In the dry lowland areas they may account for more than half of the annual rainfall.

The occurrence of winter cyclones and *kona* storms in Hawaii is closely related to the general circulation. Yeh et al. (1951b) have shown that winter rainfall in Hawaii increases as the latitude of the jet stream increases, unless the latter penetrates to the latitude of the islands themselves. They explained that when the jet stream is weak and far to the north, Hawaii will experience a period of low zonal index. Low index

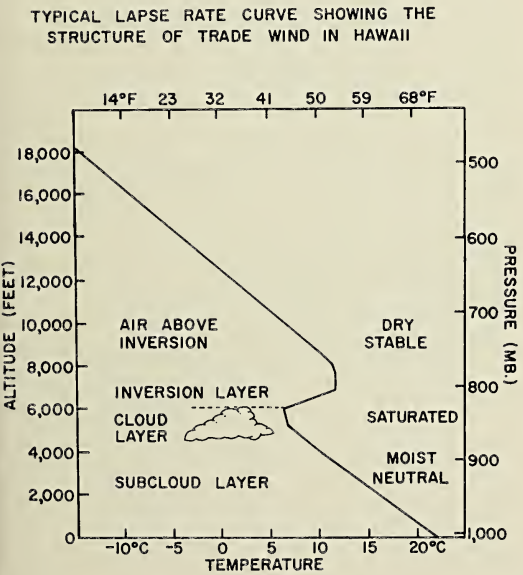


FIG. 2. Structure of the trades in Hawaii.

flow pattern is characterized by large meridional flow and frequent interaction between tropical perturbations and troughs in the westerlies.

On a hemispherical scale the mid-tropospheric westerlies are composed of roughly sinusoidal waves. In winter an upper air trough is climatologically anchored off the east coast of Asia. The location of the next downstream trough depends upon the zonal velocity according to the well-known Rossby formula. The zonal velocity in the western Pacific is such that the trough is usually located to the west of the islands in January and to the east in February (Namias and Mordy, 1952). Since the trough is characterized by convergence ahead and divergence behind, cyclones in Hawaii are more numerous in January than in February. The low rainfall in February is especially evident in the

northern island of Kauai (Leopold and Stidd, 1949).

The easterly waves are trade-wind perturbations that may form during any part of the year but with a maximum during summer. In August the easterly waves occur along the east coast of Hawaii every 3 or 4 days, bringing with them decks of high clouds and rainfall; however, they dissipate readily over the rugged land and seldom reach Oahu and Kauai.

Since 1904 there have been only four tropical storms with wind of 74 mph or more passing through the islands, all in the 1950's. The formation of a hurricane in the central Pacific is somewhat of a climatic anomaly and requires a combination of favorable conditions. In 1957, when two hurricanes passed through Hawaii, Frazier (1957) noted that a well-developed

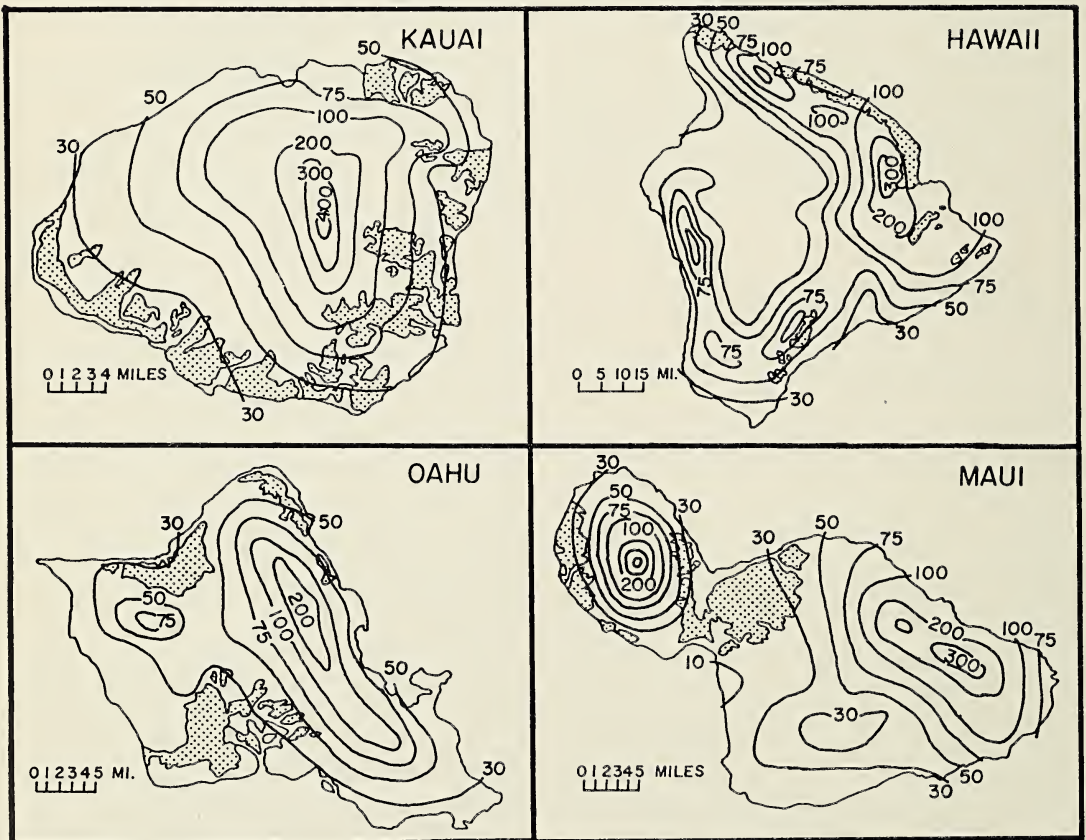


FIG. 4. Median annual rainfall (inches) in Hawaii.

trough extending to low latitudes persisted along the west coast of North America throughout the summer and fall season. This trough, through an energy dispersion mechanism, sharpens the next downstream subtropical trough, thus promoting cyclogenesis in the latter area (Ramage, 1959). The increase in radiation and temperature in Hawaii during the last decade, which will be discussed in a later section, was probably also an important cause for the increased hurricane activity.

RAINFALL

If the islands of Hawaii did not exist, the annual rainfall-over the ocean would be in the neighborhood of 30 inches; the actual average rainfall over the islands is about 70 inches. This increase of 40 inches of rainfall is the result of orographic uplifting of trade wind and its perturbation-easterly waves. The effect of easterly waves is strongest near Hilo and diminishes northward toward the Hamakua coast. The median annual rainfall at Hilo is 139 inches, considerably higher than any other coastal area in the state (Fig. 4).

The trade-wind rainfall increases with altitude exponentially up to a certain point and then decreases again. The belt of maximum rainfall varies from 3,000 to 4,000 ft, depending upon the effect of local topography on the flow patterns. This effect has been discussed in detail by Leopold (1949). The steep isohyetal gradient in a trade-wind climate is best illustrated in Kauai, where Mt. Waialeale, with a mean annual rainfall of 465 inches, is only 15 miles away from the semiarid west coast. Most of the sugar plantations are located in lowlands with a median rainfall of less than 50 inches. A few cane-growing areas on Hawaii, however, receive as much as 200 inches of rainfall in a year.

Except along the Kona coast of Hawaii, where the upslope sea breeze produces frequent summer afternoon showers, winter is the wet season throughout the state. The contrast between summer and winter rainfall is most accentuated in the dry lowlands, where the monthly rainfall in summer is often less than 0.5 inch. Summer rainfall minima are found only in a very few places in the tropics and are designated as "As" climate in the Koppen classification.

In spite of the large areal and seasonal variations, the rainfall distribution for any particular month bears a close resemblance to that of the annual. Thus Stidd and Leopold (1951) were able to express the monthly rainfall as a function of annual rainfall in the following manner:

$$y = a(x - 30) + b$$

where y is monthly rainfall; x , annual rainfall; a , the gradient factor of observed orographic increase of rainfall through increment of average annual rainfall; b , a geographic constant quantity derived from a rainfall blanket of uniform thickness over the islands and adjacent ocean. The constant 30 is inserted because the minimum annual rainfall in the dry lowland is about 30 inches.

This same concept was later expanded to describe daily rainfall distribution during trade-wind weather. For the island of Oahu, for example, a dry index of zero is assigned to a theoretical station having a zero mean annual rainfall, and a wet index of 100 to a station having 250 inches mean annual rainfall. A daily forecast chart is constructed by plotting the indices as the abscissa and the daily rainfall amounts as the ordinate. The forecaster forecasts the daily rainfall for the dry and wet index stations. From the straight line connecting these two reference points, daily rainfall for any actual station may be read off as the ordinate corresponding to the abscissa of the station's mean annual rainfall.

The trade-wind rainfall is more likely to occur during the night or in early morning than during the day. Loveridge (1924) attributed the nocturnal rainfall to the radiative cooling at the top of the clouds. Leopold (1948), however, added that cooling at night would lower the condensation level. Nocturnal rainfall, in distinct contrast to afternoon showers in many tropical countries, is in many ways beneficial to agriculture.

Trade-wind showers are very light, with drop size less than 2 mm in diameter (Blanchard, 1953), and with intensities usually much less than 0.2–0.3 inch per day. Only *kona* storms and hurricanes are capable of causing severe crop damage. On January 24, 1956, a *kona* storm deposited 38 inches of rain at Kilauea, Kauai. Such severe storms are rare, however, averaging

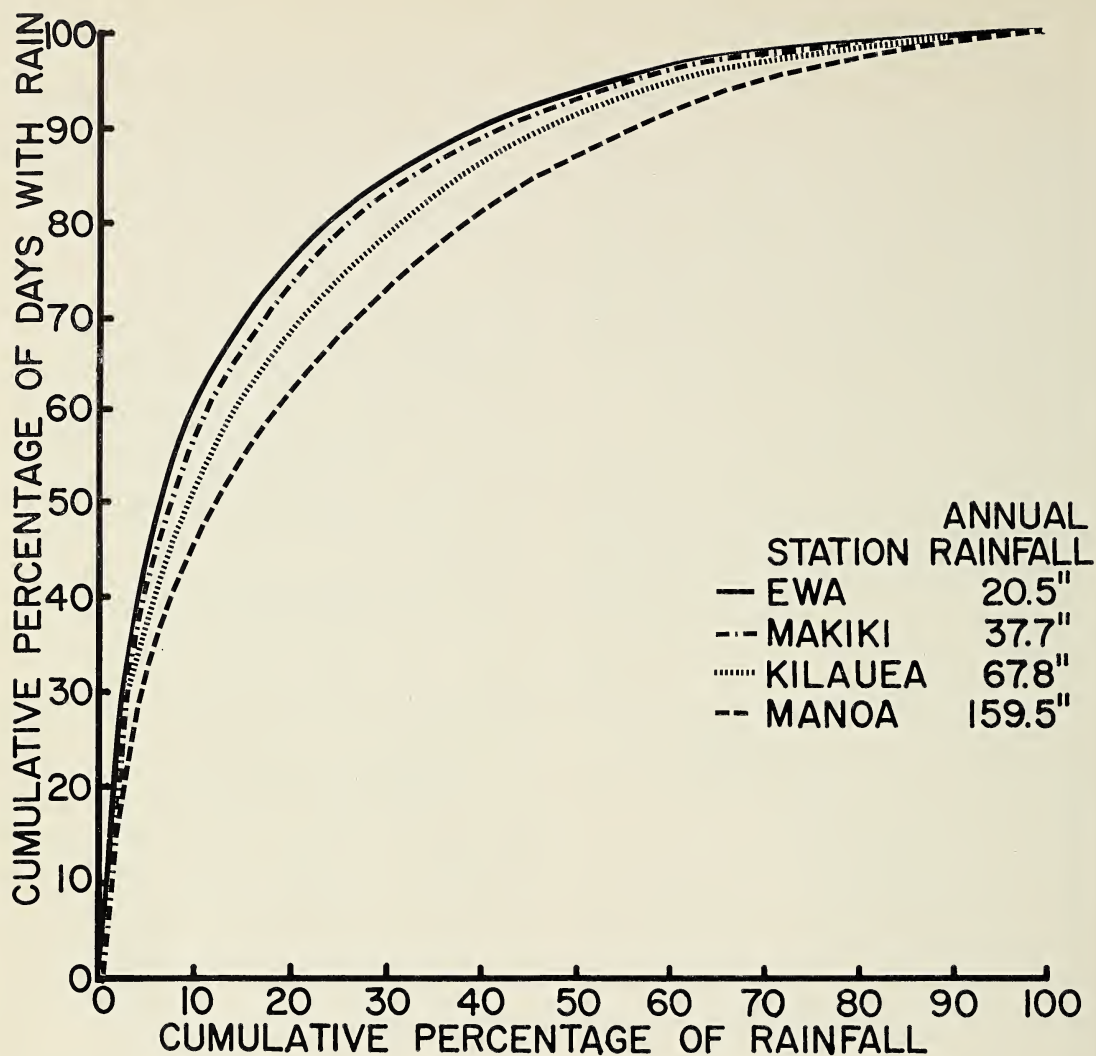


FIG. 5. Relationship between per cent of days with rain and per cent of total rainfall.

one in every 5 or 6 years. Furthermore, storm damages are usually restricted to Kauai and the east coast of Hawaii.

The frequency distribution of daily rainfall in Hawaii is extremely skewed. Figure 5 shows the relationship between the percentage of rainy days and the percentage of rainfall amounts cumulated from the least to the heaviest. At Ewa, for example, 10% of the days with the heaviest rain accounted for nearly 60% of the total, while 50% of days with least rainfall amounted to only 6% of the total rain. The skewness of the daily rainfall frequency curve

decreases slightly with the increase of annual rainfall.

The skewed rainfall distribution has at least two important implications. First, a large amount of the annual rainfall will probably be lost as runoff. Second, the mean monthly rainfall will be considerably higher than the median, and the former is a poor indicator of the "normal" condition. For this reason median rainfall is used extensively in Hawaii.

As rainfall variability is very high in the tropics (Biel, 1929), even the use of the median is inadequate for many agricultural pur-

poses. A knowledge of the extremes and frequency probabilities is indispensable. Because the basic cause of rainfall variation in Hawaii is rather uniform, the rainfall probabilities for different stations can be related in a simple, empirical manner (Landsberg, 1951). Figure 6 shows the probabilities (slanting lines) of having an annual amount of less than a given quantity (ordinate) as a function of the median annual amounts (abscissae), based on at least 60 years' records of 20 plantation stations. It is evident that Figure 6 could be used as a risk chart. Monthly rainfall probabilities could also be presented in the same manner.

TEMPERATURE

The mean annual temperatures in the lowland plantation areas vary from 72.5 F along the east coast of Hawaii to 75 F for the drier stations. The temperature decreases with eleva-

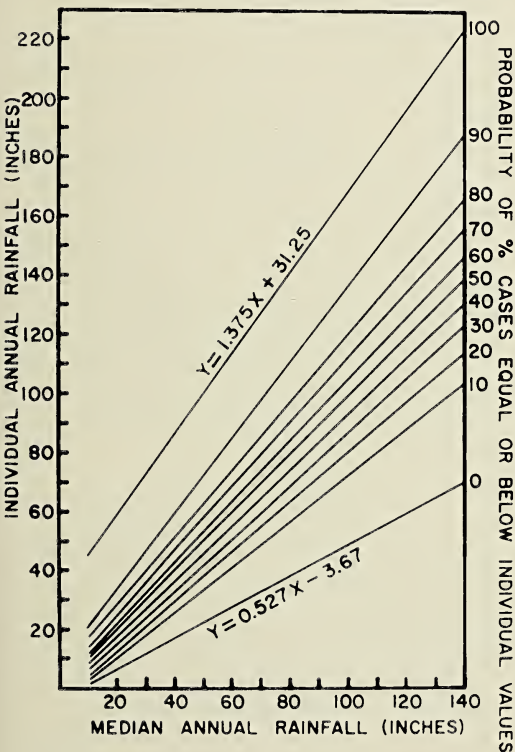


FIG. 6. Probabilities of having individual rainfall amounts in Hawaii as a function of median annual rainfall.

tion at an average rate of 4 F per 1,000 ft. The coldest plantation stations, at an elevation of about 3,000 ft, have a mean annual temperature of 62–63 F.

All the stations in Hawaii below an altitude of 5,000 ft have an annual temperature range of less than 9 F (Jones, 1942); thus a station at an elevation of 2,000 ft with an annual temperature of 65 F would have a minimum monthly temperature as high as 62 F. The isothermal climate is favorable for the growth of a perennial crop like sugar cane.

In Hawaii, as in many other tropical countries, the daily temperature range exceeds the annual mean daily temperature range and exhibits greater areal differences than does the mean annual temperature. Figure 7 shows the distribution of the annual mean daily temperature range in the cane-growing areas. In general the dry leeward stations have the greater temperature range. The daily temperature range is subject to a small seasonal variation, being slightly higher in the winter. According to the results of phytotron experiments at the California Institute of Technology, daily temperature range exerts a profound influence on fruit quality (Went, 1957).

The distribution of soil temperature in the tropics can be deduced fairly accurately from observations of air temperature (Chang, 1958). The mean annual soil temperature at any depth differs only slightly from the mean annual air temperatures. The annual temperature range at the soil surface under the cover of a sugar-cane crop is reduced to half of the air temperature range. Thus, in most of the lowlands in Hawaii soil temperature exceeds 72 F throughout the year. Studies at the Experiment Station have established that temperatures of 62 F are extremely limiting for cane growth and nutrient- and water-uptake. Such low temperatures are observed only in the mountains above 2,000 ft. The lowest soil temperature recorded on sugar cane land was 61 F at Hamakua plantation at an elevation of 3,000 ft.

RADIATION

Radiation measurements have been taken at 35 plantation stations by photochemical tubes which use oxalic acid as agent and uranyl sul-

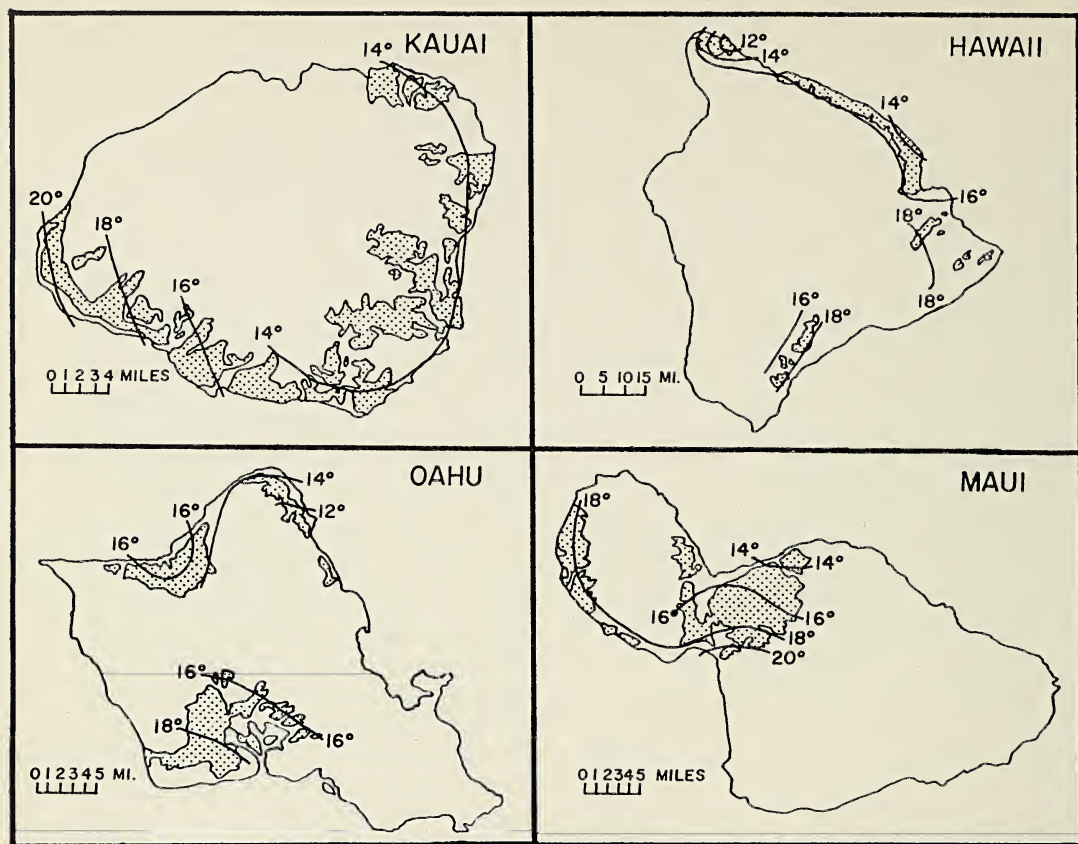


FIG. 7. Annual mean daily temperature range ($^{\circ}$ F) in Hawaii.

fate as catalyst. The photochemical method is accurate enough for general agricultural purposes (Chang, 1961). Apart from the direct effect on local climate and plant growth, the radiation data could be used for assessing yield potential, estimating irrigation water needs, directing fertilizer practices, etc. (Borden, 1940).

Figure 8 shows the distribution of mean daily radiation in Hawaiian sugar plantations. Maui has the highest radiation. Pukalani, in central Maui, receives 607 langley/day or over 220,000 langley/year. This is exceeded only by a very few desert areas in the world (Budyko, 1958). The average radiation for the cane-growing areas in Hawaii is in the neighborhood of 510 langley/day, well above Houghton's (1954) estimate of 415 langley/day for the land areas in the latitudinal zone 0° – 20° N.

In Hawaii the minimum radiation is recorded

in December, while the maximum is usually in June or July. The maximum monthly radiation is about 15% higher, and the minimum some 25% lower, than the annual mean. Radiation in December is about two-thirds that of June or July.

SECULAR CLIMATIC CHANGES

Since the cause for climatic variation in Hawaii is rather uniform, and since the leeward stations in particular are sensitive to circulation regimes (Landsberg, 1951), the climatic change at Makiki, in Honolulu, can be considered to illustrate that of the islands in general.

The average daily radiation at Makiki increased some 10% from 491 langley/day in the 1930's to 544 langley/day in the 1950's (Fig. 9). The rising trend probably started in 1936, but records before 1932 are not available.

Increased radiation results in a rise of temperature, though with a large time lag in a maritime climate. The temperature at Makiki (Fig. 10) did not start to rise until 1948.

Increased radiation could conceivably bring about a change in general circulation. Wentworth (1949) noted that the prevailing wind in Honolulu shifted from northeast to east from 1907 to the late 1930's and veered back thereafter. Increased frequency of east wind suggests a southerly location of the subtropical anticyclone, less frequent trade-wind weather, but not necessarily an increase in cyclonic activities; therefore, the trade-wind rainfall should decrease when the east wind is prevalent. At Makiki there was a trend to decreased rainfall from the 1920's to 1941 and to increased rainfall thereafter (Fig. 11). This explanation of

the rainfall trend is tentative, however, and requires further study.

Whatever the causes for climatic change may be, its impact on agriculture is varied and profound. In general, the climate in Hawaii has become more favorable for sugar-cane culture during the last 20 years. This must account for part of the yield increase during that period.

MODIFICATION OF CLIMATE

The climate of Hawaii is, in general, well suited to the growth of sugar cane. Water economy is the one area where the climatic environment could be altered significantly to bring about a higher yield. Irrigation in the Hawaiian sugar industry started in 1852. At the present time 54% of the plantation area is irrigated. In

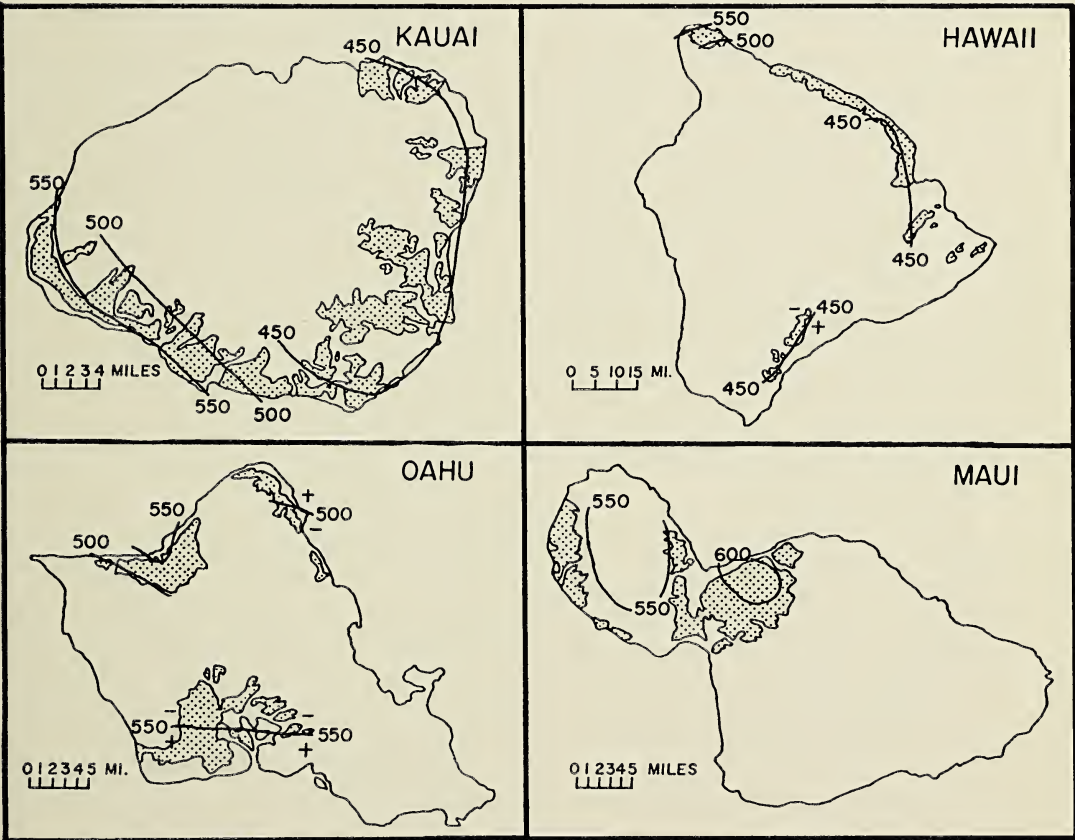


FIG. 8. Solar radiation (langleys/day) in Hawaii.

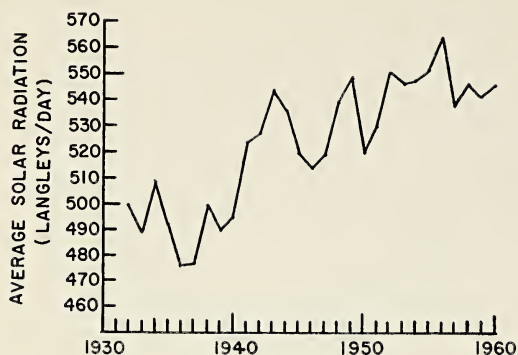


FIG. 9. Solar radiation at Makiki, 1932-60.

general the irrigated areas have less than 60 inches of rainfall in a year.

Intelligent management of irrigation requires a knowledge of the water need by a particular crop. Das (1936) advocated the use of day-degree as a measure of water need and as a guide to irrigation interval control. Numerous field experiments were conducted in Hawaii to determine the relationship between sugar yields and the number of day-degrees between irrigation. It was found that temperature is a poor indicator of the solar energy, which determines to a large extent the water needs of a crop. In fact, the monthly temperature and radiation at Makiki for the period 1932-60 have a correlation coefficient of only 0.57. The correlation is even poorer when the maximum temperature is used instead of the mean. In other parts of the world also, the use of day-degree as a phenological index has been refuted (Schneider, 1952; Wang, 1960).

As interest in the day-degree approach waned, Bayer (1954) properly called attention to the rapid development of the evapotranspiration and other micrometeorological concepts and their application in irrigation. He contended that the meteorological approach has the advantage of simplicity of operation when compared with methods based upon measurement of soil moisture change. More important, however, are the many applications of evapotranspiration in determining the regional water balance and in disentangling the climate-yield relationship. With these ideas in mind the Ex-

periment Station started an intensive study of micrometeorology in 1957.

EVAPOTRANSPIRATION AND ENERGY BUDGET

Sugar cane is a tall, ungainly plant with an aerodynamically rough canopy. Wind profile measurements indicate that the roughness parameter of a mature sugar cane of 4 cm height is 9 cm, as against 2.3 cm for thick grass of 10 cm height and 0.1 cm for short lawn grass (Sutton, 1953). The high roughness of a sugarcane crop renders the aerodynamic approach to evapotranspiration a difficult task (Deacon et al., 1958). This, together with the lack of a suitable instrument for measuring vapor flux, accounts for the fact that the aerodynamic method was not assayed in our experimental work.

The potential evapotranspiration of sugar cane was measured by drainage lysimeters and the data were analyzed by the IBM computer according to the Penman (1948) and Thornthwaite (1948) formulae. Detailed discussion of the instrumentation and the results has been reported elsewhere (Chang, 1961). It needs only to be emphasized that in a tropical mari-



FIG. 10. Five-year moving mean of temperature at Makiki, recorded at middle year, for the period 1918-61.

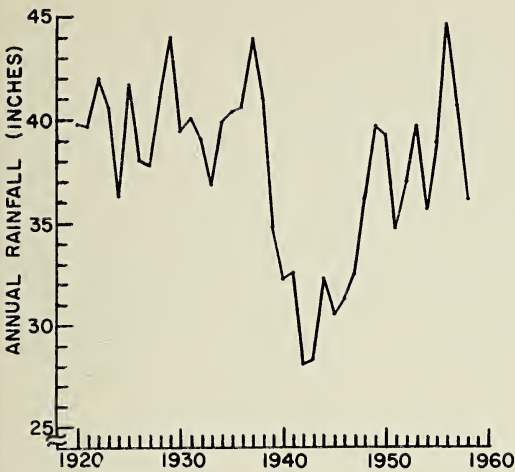


FIG. 11. Five-year moving mean of rainfall at Makiki, recorded at middle year, for the period 1920–58.

time climate the Penman estimates are far better than the Thornthwaite formula.

The various radiation components were measured at Makiki to evaluate the energy budget approach to evapotranspiration. Over a mature cane field the partition of incoming radiation is approximately as follows: 16% reflected radiation, 17% back radiation, and 67% net radiation (Fig. 12). The relationship between the net and incoming radiation is almost a constant throughout the year and over different vegetative surfaces. It was observed at Wahiawa that over short grass and pineapple fields, which have an albedo of about 5%, the net radiation remains two-thirds of incoming radiation. Theoretically it is difficult to reconcile the fact that the net radiation is not affected by the decrease of albedo, but from a practical standpoint this is convenient.

In the tropics, especially under the cover of tall vegetation, heat flux to and from the soil is negligible; therefore, the net radiation is consumed either in heating the air or in evapotranspiration. At Makiki 82% of the annual net radiation, or 55% of the incoming radiation, is used in evapotranspiration. There is a small seasonal variation of this percentage value, which is some 10% higher in summer than in winter.

There is also a regional variation of the

energy partition. For instance, the percentage of insolation used in evapotranspiration increases with total radiation. In Hawaii the regional variations of energy budget are rather small, and the equation at Makiki could be used to estimate with reasonable accuracy the monthly potential evapotranspiration for other cane-growing areas in Hawaii. For estimating short term, say weekly, potential evapotranspiration it is advisable to use an evaporimeter which integrates not only radiation but other meteorological elements as well.

The simple energy budget presented here is applicable only in the humid tropics. In middle and high latitudes the energy budget is subject to enormous seasonal variations. In an arid climate the advective heat, which is extremely difficult to evaluate, may introduce a significant error.

PAN EVAPORATION AS A MEASURE OF EVAPOTRANSPIRATION

Until a cheap and readily installable piece of equipment capable of recording vertical vapor transfer is available, agricultural meteorologists will continue to use evaporation pans. In an arid climate pan evaporation is accentuated by the oasis effect to such an extent that its usefulness as a climatic parameter is greatly impaired. In humid climates, pan evaporation has been found to be more accurate than the Penman and Thornthwaite estimates (Suzuki and Fukuda, 1958), and a satisfactory guide to irrigation control (Krogman and Lutwick, 1961). In this

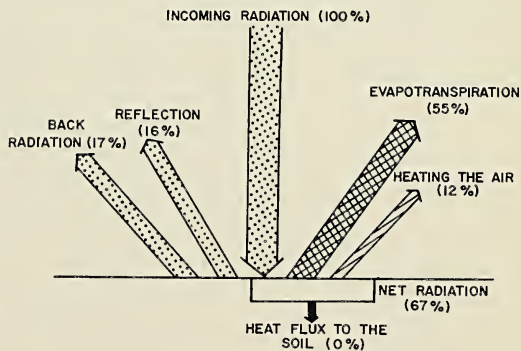


FIG. 12. Energy budget over a sugar-cane field at Makiki.

respect Hawaii is ideally suited to the use of evaporation pans, thanks to the existence of a moist mixing layer below the trade inversion.

Lysimeter and pan-evaporation records in Hawaii indicate that the potential evapotranspiration of mature sugar cane is approximately the same as evaporation from a ground-level U.S. Weather Bureau Class A pan. The ground-level pan, however, evaporates some 10% less than an elevated pan at cane top level, and some 15% more than a buried pan in an irrigated plot.

The one-to-one ratio obtained by using the ground-level pan is very much in line with ratios found for many other crops. From the standpoint of water use, crops may be divided into two groups: conventional and nonconventional. The potential evapotranspiration of a nonconventional crop is influenced to a large extent by its physiology. Rice, with a ratio of 1.2 (Suzuki and Fukuda, 1958), and pineapple, with a ratio of 0.35, are good examples. The water need of a conventional crop is determined primarily by the weather conditions, although it increases with the roughness of the crop, especially in areas of large advective heat (Tanner and Pelton, 1960). Thus the ratio increases from 0.75 for short grass (Penman, 1948) to 0.87 for corn (Fritschen, 1960*a*), and to 1.0 for sugar cane.

The fact that potential evapotranspiration of sugar cane approximates pan evaporation does not necessarily mean that irrigation based on a ratio of one-to-one is most economical. A new experiment has been set up at Waipio to determine sugar-cane growth and yield by using different pan ratios, i.e., 1.30, 1.15, 1.00, 0.85, 0.70, and 0.55. The yield data over a number of years should permit determination of the most economical level of irrigation.

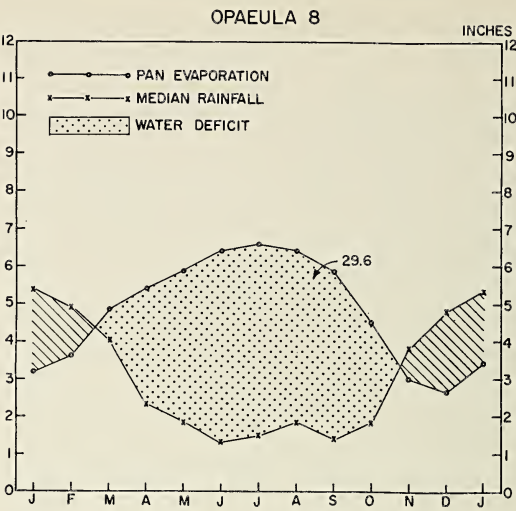


FIG. 13. Monthly water balance at Opaepala.

MONTHLY AND ANNUAL WATER BALANCE

The monthly water balance of a place can be portrayed by comparing the pan evaporation and the median rainfall. At Opaepala, for example, rainfall exceeds pan evaporation during the winter months from November to February (Fig. 13). From March to October, however, supplemental irrigation is needed to fill the water deficits, which total 29.6 inches in a year.

By analyzing the water balance of some 30 stations we have been able to construct an annual water-deficit map for the cane-growing areas in Hawaii (Fig. 14). The map is tentative, as the stations are not well distributed. Recently we have added 20 pan stations in order to strengthen the network. In constructing the map the radiation records were also used to fill the gap.

By planimetry the deficit areas in the map,

TABLE 1
ESTIMATED ANNUAL WATER DEFICIT FOR GROWTH OF SUGAR CANE

ISLAND	AREA (acre)	AVERAGE DEFICIT (inches)	TOTAL DEFICIT (acre-inches)
Hawaii	98,601	16.5	1,628,390
Maui	42,424	72.8	3,087,612
Oahu	33,223	41.0	1,361,141
Kauai	47,088	33.4	1,573,502
Total	221,336	34.6	7,650,645

the annual water deficits of the four islands are estimated as in Table 1. It is noted that there is a large regional variation. The average annual deficit for plantation areas on Hawaii, which are almost exclusively unirrigated, is only 16.5 inches. By contrast, the average deficit for Maui is as high as 72.8 inches.

The total annual water deficit for all the plantations is estimated at 7.6 million acre-inches, or 208 billion gallons. The industry uses about 400 billion gallons of water a year for irrigation. At first glance, the cane crop in Hawaii seems to be irrigated more than adequately. This is, however, not true. Much of the irrigation water is wasted due to maldistribution. For instance, a plantation irrigation at a high level of adequacy often loses as much as 60% of its water through deep penetration or runoff. Fur-

thermore, the water supply is often such that a plantation over-irrigates in one season and suffers from drought in another.

The monthly water-balance charts and the water-deficit maps are a valuable guide to agricultural planning. Such questions as whether or not to construct a reservoir, what irrigation system to adopt, and what crop to grow can be answered, at least in part, through the use of climatic data.

The monthly water balance presented above is by no means precise because the median rainfall is only an approximation of the effective rainfall. The amount of effective rainfall varies with the rainfall intensity as well as with the moisture storage capacity of the soil. To credit rainfall correctly, it is necessary to compute the daily water balance.

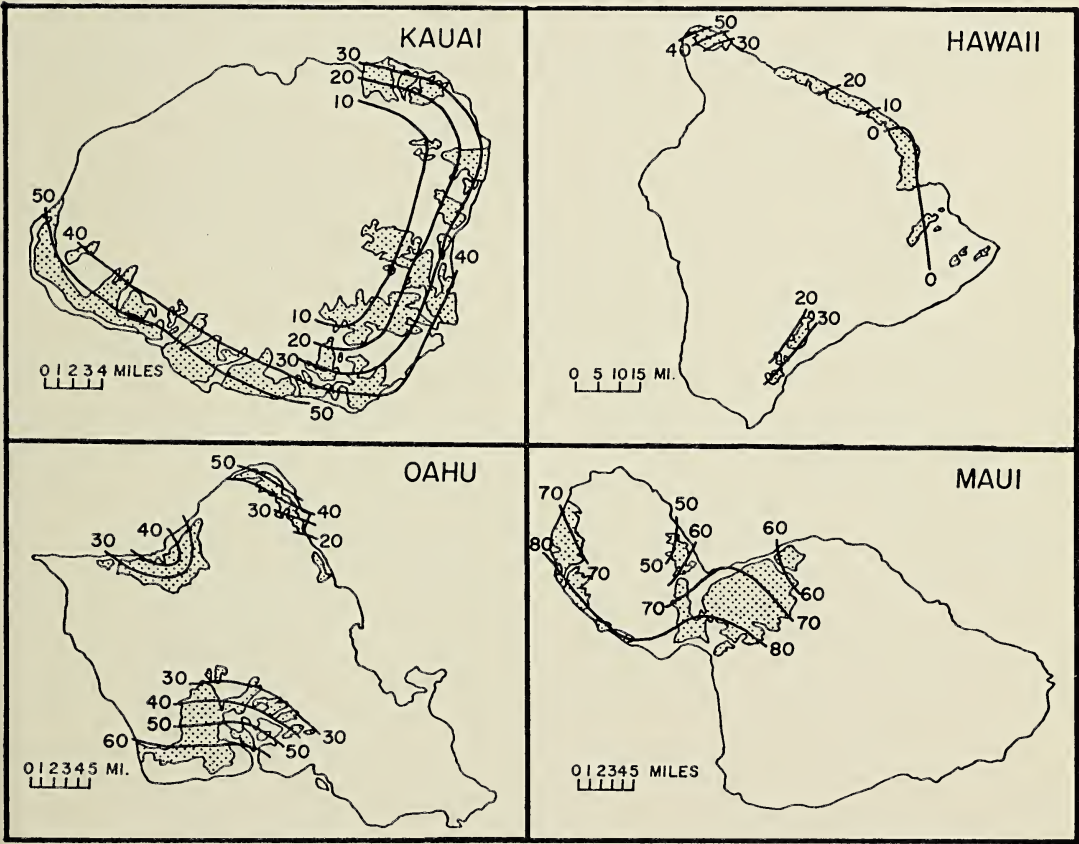


FIG. 14. Annual water deficit (inches) in Hawaii.

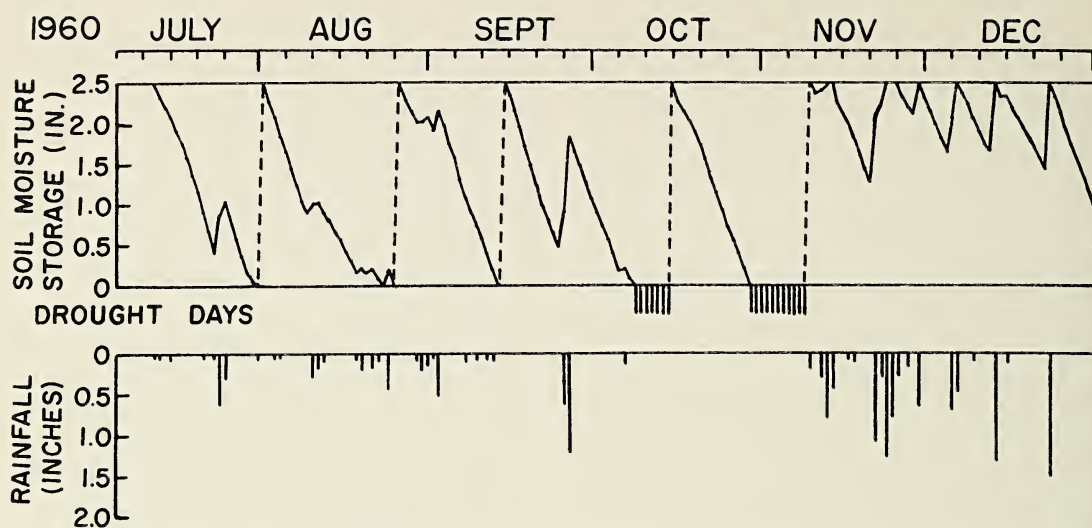


FIG. 15. Running daily soil-moisture balance at Waipio. Dashed lines indicate irrigation.

DAILY WATER BALANCE

If the soil storage capacity is known, the daily water balance can be computed by comparing the daily rainfall and potential evapotranspiration. Figure 15 shows the running daily soil moisture balance at Waipio, where the storage capacity is 2.5 inches. The rainfall in excess of the amount that a soil can hold is regarded as surplus. By subtracting the surplus from the rainfall, the effective rainfall can be determined. When the daily water balance reaches zero, drought occurs and irrigation is called for. The water deficits during the drought days can be added to determine the total water deficit during the growing season of a crop.

This daily water-balance scheme assumes that the depletion rate of soil moisture is equal to potential as long as the soil moisture is above the wilting point. This assumption is adopted primarily for simplicity of computation. It should not be taken to mean that we endorse the well-known Veihmeyer and Hendrickson argument (1955). Although the relationship between the depletion rate and the moisture tension is still debatable, there are indications that the relationship probably varies with weather conditions (Denmead, 1961). The constant depletion rate reported by Veihmeyer and Hendrickson is probably less in error in a humid, cloudy climate, especially under the cover of

tall vegetation, than in a dry continental climate.

The computed daily water balance at Waipio has been compared with gypsum-block readings. They agree in general. When the water balance reaches zero, the gypsum-block resistance is usually between 3,000 and 5,000 ohms. The latter value calls for irrigation. In general, the irrigation date determined by the pan evaporation is one or two days earlier than that indicated by the block reading.

KOHALA RESULTS

Kohala is a plantation on northern Hawaii with an annual water deficit varying from 20 to more than 50 inches. In 1960 only about 27% of the plantation was irrigated. The question then arises as to whether an expanded irrigation program will be profitable in the long run. Apparently this question cannot be answered without an investigation of the climate-and-yield relationship.

The daily water balances during more than 10 years for one irrigated and five unirrigated stations in Kohala were computed by using a storage capacity of 3 inches. The total water deficits for different crops were summarized and correlated with the yields (Fig. 16). The correlations are highly significant for Hawi, Niulii 9, Halawa 3, and Upolu 6, but are poor for Puakea 6 and Union 8. In general they are very good for field crops, especially in view of

the fact that there were considerable differences in crop age, solar radiation, cultural practice, variety, etc.

The average slope of the regression lines for the five unirrigated fields is 4.6 tons of cane per acre for every 10 inches of water. This is an important figure in determining the economy of irrigation. It is thought that by extending the regression lines to the point of zero deficit the approximate yield potential of the area could be estimated. The average yield for the five unirrigated fields was 65.2 tons of cane per acre. The estimated potential would be 91.4 tons cane per acre, or an increase of 40% over the present yield. This estimate is probably reasonable when compared with the yield of 109 tons of cane per acre at Waialua, Oahu, an irrigated plantation with slightly better climatic conditions.

Admittedly the use of linear extrapolation as a means of estimating yield potential is a crude procedure. Yet this seems to be the most reasonable method we can adopt at present. Theoretically the relationship between water and yield should be curvilinear, as shown in Figure

17. The exact shape of the curve cannot be determined until results of the Waipio experiments become available. The difference in yield potential between the two curves in Figure 17 is caused primarily by radiation, if soil and other factors are constant. Experiments are also underway to assess the effect of solar radiation on yield. It is hoped that in future this concerted research program will enable us to draw with certainty the climate-and-yield relationship now presented hypothetically in Figure 17.

By analyzing the daily water balance at Kohala, we also derived an empirical relationship between the actual rainfall and the effective rainfall for plant use. The computation was carried out by assuming varying soil-moisture storage capacities of 2, 3, and 4 inches. Figure 18 shows the curvilinear relationships between the annual rainfall and effective rainfall for all the five stations combined. Multiple regression analyses were carried out to the fourth power and a few selected values are given in Table 2. It is noted that the effective rainfall increases with the storage capacity only slightly, espe-

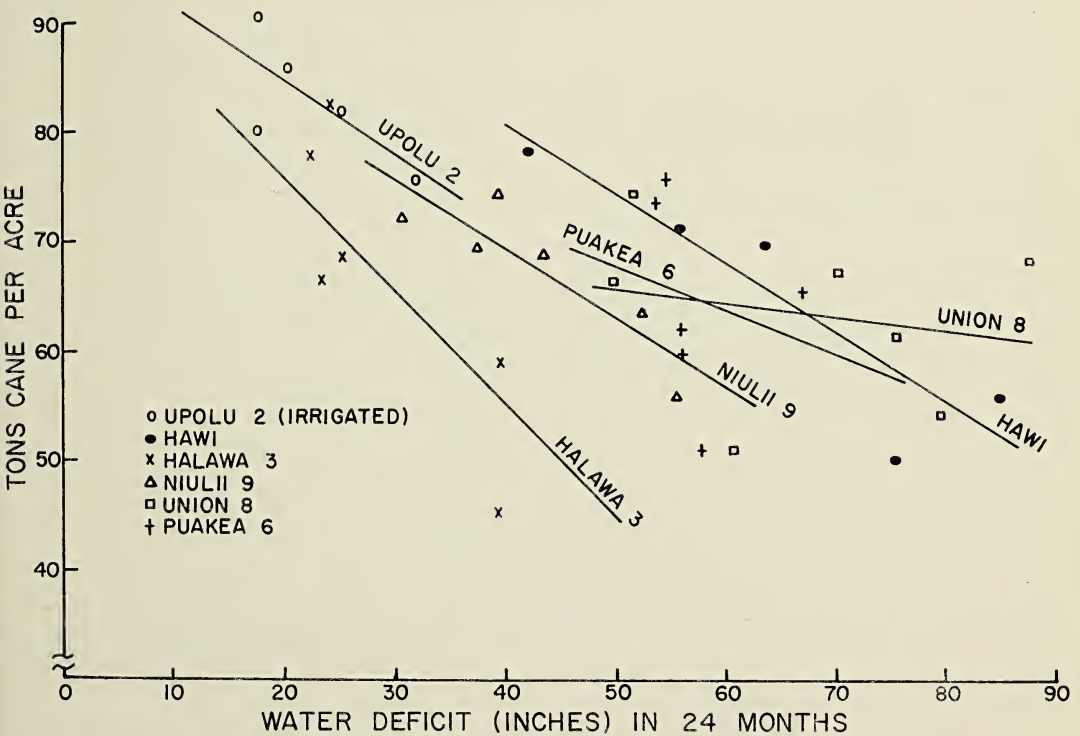


FIG. 16. Relationships between cane yield and water deficit for six fields at Kohala.

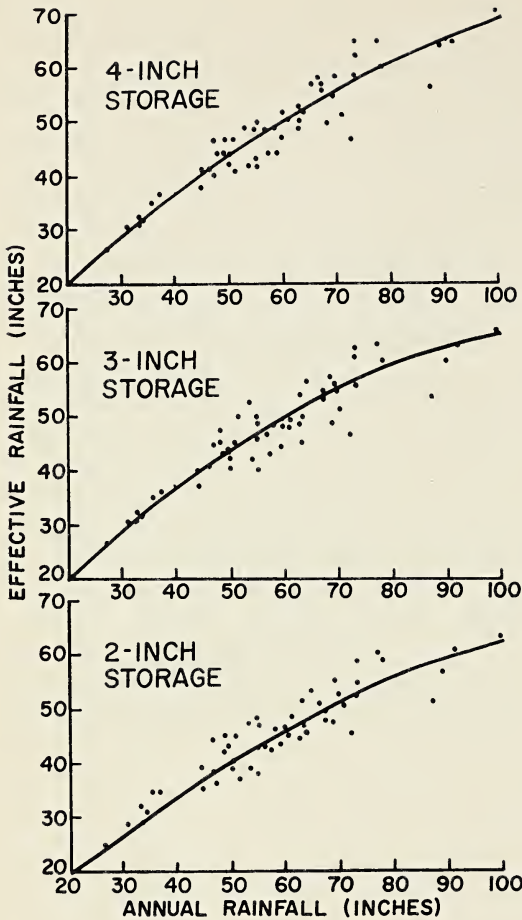


FIG. 17. Hypothetical curves showing the relation-
ship between cane yield and climate in Hawaii.

cially when the annual rainfall is low. The Kohala results could be applied to other areas for estimating effective rainfall, as the rainfall characteristics are more or less similar throughout the islands.

JUICE QUALITY

The dry matter production of a sugar-cane crop can be related in a quantitative manner to the solar radiation and the amount of effective water applied, if cultural practices remain the same. The problem of juice quality is more complicated, however, and at present can be dealt with only in a rough empirical manner.

The weather factors that favor high sucrose content are:

1) High radiation favors photosynthesis and formation of sucrose.

2) Water supply should be adequate during the growing season, but should be followed by a dry period of about two months before harvest. High rainfall during the ripening period will dilute the juice and cause a part of the sucrose to break down into other sugars.

3) It is generally known that cool weather preceding the harvest season improves the sucrose content of the cane. Less well known, however, is the beneficial effect of large diurnal temperature range. Harrington (1923) and Morinaga (1926) have shown that alternating high and low temperatures hasten the germination of seeds and bulbs. If the buds of sugar cane react as favorably towards a great range of temperature, then earlier suckering could be expected, which would mean a greater number of mature stalks at harvest and hence a higher sucrose content.

In summary, the ideal weather for high juice quality would be abundant sunshine, high temperature range, adequate water supply during the growing season, and dry and cool weather during the ripening period. A study of Figures 7 and 8 would indicate that the Ewa, HC&S, Pioneer Mill, and Kekaha plantations have the best climate for good juice quality.

It is true that we cannot modify the climate to such an extent as to appreciably improve the juice quality. Nevertheless, an understanding of

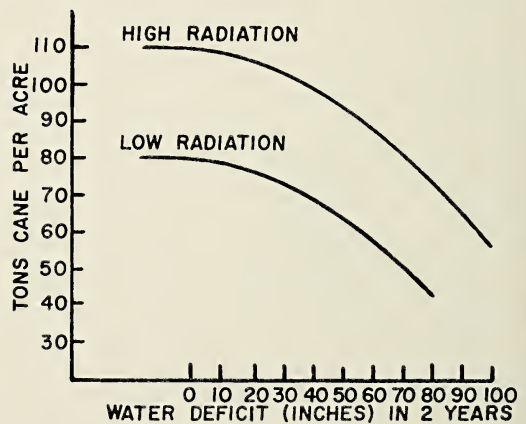


FIG. 18. Relationships between annual rainfall and effective rainfall in Kohala, assuming varying soil-moisture storage capacities of 2, 3, and 4 inches.

TABLE 2

EFFECTIVE RAINFALL AS A FUNCTION OF ANNUAL RAINFALL AT KOHALA
(Assuming varying soil moisture storage capacities of 2, 3, and 4 inches)

Annual rainfall (inches)	40	50	60	70	80	90	100
Effective rainfall for:							
2-inch storage	34	40	46	52	56	60	61
3-inch storage	37	43	49	55	58	62	65
4-inch storage	37	44	50	56	60	65	69

the climatic effect on juice quality has at least two practical applications. First, we can schedule planting and harvest dates accordingly, in order to best fit the seasonality of a climate; in this connection a study of climatic singularity would be valuable. Second, an understanding of the role played by climate could help us to interpret the results from many agronomic experiments.

CONCLUDING REMARKS ON CLIMATOLOGICAL RESEARCH

This review has demonstrated the broad scope of climatological research in the Hawaiian sugar industry. The application of this research, as Curry (1952) pointed out 10 years ago, could ultimately give new life to many an economic activity. Toward that end we have made only a beginning. Much work remains to be done. Future research should be planned in three general areas:

1. **GENETIC CLIMATOLOGY:** Only 20 years ago climatology was treated primarily as a study of statistical meteorology, replete with records but almost devoid of explanations. The post-war studies of the climate of Hawaii are among the pioneers in the field of genetic climatology. These studies bring a fair measure of systematic order into the otherwise incoherent climatic facts and explain many seemingly local phenomena in the light of general circulation. A better understanding of the dynamism and genesis of climate could conceivably lessen or avert agricultural hazards in many other parts of the world. It is hoped that Trewartha's new book (1961) will stimulate interest and hasten development in this field.

2. **ENERGY BUDGET AND WATER BALANCE:** Genetic climatology focuses its attention on the

free atmosphere. Local variations, caused by the interaction of the atmosphere and the terrain, can best be understood by a study of the energy budget and water balance. Conventional observations, tied to the needs of synoptic forecasting, are often inadequate for the study of topoclimate. Urgently needed is an internationally-standard field instrument for the measurement of solar radiation. The recent development of an instrument which measures net radiation (Soumi et al., 1954; Fritschen, 1960b), or even net radiation minus soil heat flow (Portman, 1954), is most encouraging.

Measurements of evapotranspiration by inexpensive field instruments are also needed on a wider scale. In humid climates evaporimeters, such as evaporation pans or atmometers (Halkais et al., 1955), have been of value. In arid climates, however, the problem is vexing. There the very concept of potential evapotranspiration is elusive and unrealistic. For potential evapotranspiration requires, by definition, a homogeneous soil moisture regime infinite in horizontal extent, and once the area upwind is adequately watered the climate is no longer arid. In actuality the effect of advective heat exists even in a very large irrigated area. Gal'tsov (1953), for instance, has observed decreasing water requirements from the border towards the center of an irrigated region in Kazakhstan. It is difficult to evaluate the effect of advective heat. Perhaps an approach similar to but more refined than Belasco's study (1952) on the modification of air mass is in order.

To solve the water-balance equation the soil moisture storage capacity needs to be known. This requires the cooperation of soil scientists. On a global scale, representative figures of moisture storage capacity of the major geographical regions are useful for many purposes.

In view of the importance of energy budget and water balance in characterizing the regional climate, it is a pity that almost all the textbooks in English on climatology make no reference to the subjects. The Russian work by Budyko (1958) is the only general reference. In this respect, Thornthwaite's sustained interest in these areas is commendable, and his recent plea (1961) should be well heeded.

3. EFFECT OF CLIMATE ON GROWTH AND YIELD: We have demonstrated that determination of water balance is a step toward solving the climate-and-plant relationship. More field experiments are needed, however, to define the hypothetical curve as presented in Figure 17. Eventually we hope that a method will be developed to estimate dry-matter yield and juice quality from climatic data.

It has been argued that climatologists are not responsible for the study of the effects of climate on vegetation (Trewartha, 1957). To be sure, plant scientists are better qualified to run the field experiments. But the development of techniques for evaluating the climatic elements that affect plant growth falls squarely within the responsibility of a climatologist. Without these techniques the meaning of climatic data is often obscured. Whoever solves the problem of climate-and-plant relationship will contribute work of enormous practical value.

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Root Development in Aluminous Hawaiian Soils¹

D. L. PLUCKNETT,² J. C. MOOMAW,³ and C. H. LAMOUREUX⁴

ABSTRACT: Roots of *Rhodomirtus tomentosa* and *Melastoma malabathricum* were excavated in three soil series from the bauxitic area of Kauai. Root systems of *R. tomentosa* and *M. malabathricum* in Kapaa and Halii soils were very shallow, with tap roots turning laterally at shallow depth and with long lateral roots very close to the soil surface. Deeper tap-root penetration of *R. tomentosa* and *M. malabathricum* was observed in the Koolau soil.

Lime and phosphorus treatments were added to bauxitic subsoils of the Kapaa and Halii series in pots and *Leucaena glauca* (L.) was planted in the pots. Tap roots of *L. glauca* were stimulated by phosphorus treatment, but were restricted in untreated subsoils. Increased root development with phosphorus treatment seemed to be more related to phosphorus supply than to decreased aluminum effects. No evidence of root damage due to aluminum was found.

L. glauca roots were sectioned with a freezing microtome and stained, using hematoxylin without a mordant. Although all staining obtained could not be attributed to aluminum, since other metals can act as mordants for hematoxylin, intensity of staining was assumed to be related to aluminum concentration in the tissues. Cell walls, nuclei, and cytoplasm stained in all tissues, and outer walls of epidermal cells stained very heavily. Staining was more intense in roots from check and P-treated plants than in roots from lime-treated plants.

STUDIES of the root development of natural plant communities (Weaver 1920, Weaver and Albertson 1943, Weaver and Darland, 1949) and of cultivated plants (Weaver, 1926; Troughton, 1957; Crider, 1955) under a variety of conditions and treatments, are well known to ecologists. Normally, a well-developed root system is essential to the vigor-

ous growth and successful competition of the dominants in most plant associations. Shallow-rooted plants, however, are known from many different habitats, especially those with poor physical properties but also from those with a low nutritional status with respect to nitrogen, phosphorus, calcium (Fox, Weaver, and Lipps, 1953) and potassium (Haynes, 1943). Root damage and restricted root development in such crop plants as barley and tobacco have been associated with high levels of soil aluminum, but little is known of root development in uncultivated plants growing in soils with high concentrations of active aluminum.

In a study of vegetation on gibbsitic Hawaiian soils Moomaw and Takahashi (1960) reported shallow root systems, but detailed studies of root development and distribution in these

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soils were not made at that time. Two particularly aggressive plant species, *Rhodomyrtus tomentosa* (Ait.) Hassk. and *Melastoma malabatricum* L., are known to grow well on Hawaiian bauxitic soils, where *Rhodomyrtus* tends to form dense thickets excluding all other vegetation. These two species were introduced on Kauai about 50 years ago and *Rhodomyrtus* has now been declared a noxious weed. It is the object of this study to characterize root growth and distribution of these and other tap-rooted species on the bauxitic soils of Kauai.

Aluminum has been shown to be toxic to plants. One of the frequently-reported toxic effects of aluminum is root injury (Lignon and Pierre, 1932; McLean et al., 1926; Bortner, 1935) in which roots may be brown in color with few rootlets and discolored root tips (Gilbert and Pember, 1931) or with root tips blackened and thickened to twice normal size (Bortner, 1935). Restricted lateral root development in rye has been reported using water cultures (Magistad, 1925). Trenel and Alten (1934) concluded that aluminum may be a root poison. Using a divided-root technique corn plants were exposed to nutrient solutions with and without aluminum. Injury was restricted to roots in the high-aluminum solutions. Nagata (1954) found that over 5 ppm aluminum in culture solutions hindered barley growth and that aluminum seemed to accumulate in the roots. Growth hindrances were decreased by adding phosphorus or calcium. He concluded that translocation of phosphorus from the root to the top in the barley plant was hindered by aluminum in culture solutions.

The precipitation of phosphate and aluminum in the plant as an aluminum phosphate has been suggested. Burgess and Pember (1923) proposed that aluminum was fixed as relatively insoluble aluminum phosphate in plants, especially in roots. McGeorge (1925) suggested that internal precipitation of aluminum by phosphorus may be important in plants but listed no specific location.

Wright (1937) divided root systems of barley plants, placing each half in different culture solutions with and without aluminum. Plant analysis indicated plant damage resulting from poorly developed root systems in solutions con-

taining aluminum, and internal precipitation of phosphorus and aluminum where large amounts of aluminum and phosphorus were present in roots. Wright (1943) found a higher percentage of phosphorus in aluminum-treated barley plants than in nontreated; this was particularly marked in the roots. The water-soluble phosphorus in the aluminum-treated plants was low, while a H_2SO_4 solution (pH 3.0) extracted practically all P from untreated plants but much smaller amounts from plants grown in contact with Al. The precipitation was listed as occurring primarily in roots, and sharp reductions in yield were attributed to P deficiency in meristematic regions due to root precipitates. Wright (1945), using microchemical tests to determine inorganically and organically bound P, found abundant inorganic P in roots grown in contact with Al and little or none in roots from solutions without Al.

Problems of plant growth on acid soils have long been ascribed to the "active" Al in the soil and to problems of phosphate nutrition due to fixation of phosphates by Al. Longnecker and Merkle (1952) studied root development of crimson clover in relation to lime placement and found most root growth in layers which had been limed. The beneficial effect of liming was attributed to decrease in solubility of Al and Mn and an increase in solubility of P. Ragland and Coleman (1959) applied lime at several rates to subsoils of the Norfolk catena in pots and found grain sorghum root growth into unlimed subsoils was related inversely to amounts of exchangeable Al. Root growth into subsoils increased substantially with lime treatment. Root development of sorghum grown in suspensions of acid clay was restricted severely unless 80% of the acidity was neutralized.

DESCRIPTION OF EAST KAUAI

The area studied is referred to by McDonald et al. (1960) as the Lihue Depression. It is a nearly circular basin with the rim being formed by the Haupu ridge on the south, the main mountain mass of central Kauai on the west, the Makaleha mountains on the north, and Nonou and Kalepa ridges on the east. The basin is floored with lavas of the posterosional Koloa

volcanic series. Two vents from the Koloa volcanic series, Hanahanapuni Crater and Kilohana Crater, lie within the basin.

The general topography of the basin is of gently sloping to moderately steep ridges and plains dissected by perennial streams, notably the Wailua River and its tributaries.

The average annual rainfall in the Lihue Depression ranges from 40 or 50 inches near the ocean to over 170 inches near the mountains. Rainfall is usually highest in winter months but there are no months during which no rain falls.

Mean monthly temperatures from nine stations below 300 ft elevation on Kauai range from 69 F in February and March to about 77 F during August through October (McDonald et al., 1960). Although no temperature records are available for higher elevations, there is a decrease in temperature with increase in elevation, of about 3 F for each 1,000 ft.

Prevailing winds are the northeast trade winds but cyclonic storms occasionally upset this pattern, especially in winter months.

DESCRIPTION OF SOILS STUDIED

Three soils occurring in the Lihue Depression were selected for study. These soils are located in or near the main area of infestation of *R. tomentosa* and *M. malabathricum* and either comprise or are associated with the major bauxitic soils of East Kauai. The principal mineral form of Al present in these bauxitic soils is gibbsite, the trihydrate of aluminum oxide (Sherman, 1958). Detailed soil descriptions have been made by the Soil Conservation Service (Womack, 1960).

Kapaa Series

The Kapaa series is a deep, well-drained, Aluminous Ferruginous Latosol developed on gently sloping to steep uplands on Kauai. These soils occur mainly in association with the Halii soils which lie above, and Puhi soils which lie below. The Halii series is developed from parent material similar to that of the Kapaa series, namely the melilite and nepheline basalts of the Koloa volcanic series. The Kapaa soils occur between 200 and 1,000 ft elevation with mean annual rainfall from 60 to 100 inches. They are

clayey in texture but feel like silty clay in the A horizon (0-6 inches) owing to the strong, very fine granular structure. They are extremely hard when dry but sticky and plastic when moist, containing many roots and few pebbles in the surface layers. With depth, some mottling occurs on the blocky structures and pebbles are more numerous. These soils are used mainly for pasture, nonirrigated sugar cane, and pineapple.

Halii Series

The Halii series is a deep, well-drained Aluminous Ferruginous Latosol on gently sloping to moderately steep uplands on Kauai. This series is associated with the Koolau series at higher elevations and with Kapaa series below. It occurs in belts at about 300 to 1,000 ft elevation with mean annual rainfall from 80 to 120 inches. The A horizon (0-9 inches) of this series is a gravelly clay that feels like silty clay and is grayish-brown in contrast to the yellowish-brown of the Kapaa series. It is somewhat less hard when dry and more plastic when wet than the Kapaa. It is used principally for non-irrigated sugar cane and small acreages of pineapple.

Koolau Series

The Koolau series is a deep, poorly-drained Hydrol Humic Latosol developed on gently sloping to moderately steep uplands. It is associated with the Halii soils, and occurs between 400 and 4,000 ft elevation with mean annual rainfall of 120 and 200 inches. Most of the Koolau series is covered by rain forest, but some is used for sugar cane and pasture.

The Koolau series is a grayish-brown clay that feels like a silty clay loam, with a structure that appears to be massive to very weak medium granular. It is only slightly sticky and plastic when moist, with matted roots and many worm holes and casts making it quite porous. Lower horizons have distinct strong brown mottles.

EXPERIMENTAL PROCEDURE

Roots of *Melastoma malabathricum* and *Rhodomyrtus tomentosa* were excavated in the Halii, Koolau, and Kapaa soil series and descriptions and measurements were made of

depth of penetration of tap roots, location and length of lateral roots, relation of roots to soil profile, and possible evidence of causes of thicker formation. A few plants of Norfolk Island pine (*Araucaria excelsa*) (Lamb.) R. Bn. were also excavated in the Wailua Game Refuge.

Root description and measurement were also made of *R. tomentosa* seedlings used in a pot experiment designed to measure plant and soil Al. Notes taken included color, thickening, black tips, number of lateral roots, length of tap roots, and number of active buds.

Because tap roots were observed turning laterally in Halii and Kapaa soils in the field, a pot experiment was established using the soil layer in which these roots turned as "subsoils." These soils were collected from horizons where tap roots were observed to turn laterally and were sacked carefully to prevent dehydration. They were screened through wire mesh containing approximately 4 meshes to the inch. Weighed samples of the screened soil were used to form the "bottom" 5-inch soil layer in 11-inch plastic pots, and were treated with six lime and phosphate treatments. After the treatments were mixed thoroughly in the subsoils, a 5-inch layer of untreated Kapaa surface soil was added. *Leucaena glauca*⁵ seeds were planted in the surface soil and after germination plants were thinned to two per pot.

At harvest the soils were carefully removed from the pots and washed from the roots. Measurements of tap-root penetration and lateral root development were made. Roots were examined for blunted and blackened tips, and root tips from each treatment were preserved for staining studies. Yields of tops and roots were recorded and plant Al concentrations were determined. The pH, extractable Al, exchangeable calcium, and cation exchange capacity were determined for each soil.

Root tips of *L. glauca* plants from treated pots were sectioned on a freezing microtome and stained, using hematoxylin without a mordant (Johansen, 1940). Slides of the root sections were made and photomicrographs were taken.

⁵ In a personal communication Dr. F. R. Fosberg has indicated the correct name for this plant should be *Leucaena leucocephala*.



FIG. 1. *Rhodomyrtus tomentosa* excavated in the Kapaa soil series, Wailua Game Refuge. The tap root turned laterally at 4-inch depth and lateral roots penetrated diagonally before ascending toward the surface.

RESULTS

Six *R. tomentosa* plants were excavated in the Kapaa soil series. All plants were extremely shallow-rooted, with tap roots turning laterally at depths of from 3 to 10 inches below the surface (Fig. 1). Lateral root development in these plants was especially pronounced and one large 10-ft shrub had a lateral root 24 ft long. Lateral roots displayed a tendency to grow downward and outward for 2 to 4 inches and then to ascend toward the surface. Lateral roots were frequently found just at, or slightly under, the soil surface.

Two thickets of *R. tomentosa* were excavated in the Kapaa soil series. These thickets contained shrubs up to 10 ft in height with trunks 1.5 to 2.25 inches in diameter. Roots were observed with diameters up to 2 inches. Tap roots turned at a depth of 10 inches and no roots of the thickets were found below this depth. There was no evidence of root fusion.

M. malabathricum plants excavated in the Kapaa soil were found to have root development similar to that in *R. tomentosa*, with tap roots turning laterally at shallow depth and long lateral roots. One plant (Fig. 2) had a small, twisted and deformed tap root with 2 main lateral roots 5 ft long. Fibrous roots were almost lacking in both *R. tomentosa* and *M. malabathricum*.

Norfolk Island pine trees (*A. excelsa*) planted about 10 years ago in the Kapaa soils were

excavated to determine root development in species planted in these soils. Tap roots of these trees penetrated to what appeared to be the bottom of the planting hole before turning upward toward the surface.

Two individual plants and a thicket growth of *R. tomentosa* were excavated in the Koolau soil near Hanahanapuni Crater. Tap roots of the two individual plants penetrated 9 inches downward before turning diagonally for 1 or 2 inches. Small plants of *M. malabathricum* nearby, like the *R. tomentosa*, had tap roots which penetrated from 8 to 10 inches.

The main tap root of the *R. tomentosa* thicket penetrated 24 inches downward in the Koolau soil without turning, even though water from the soil filled the hole at a depth of 1 ft, placing it well below the water table at the time of sampling. One lateral root of this thicket was observed from which numerous stems had arisen. This was the only observation of this type in the plants excavated. It is possible that this "root" could have been a stem buried by road construction since the thicket was located close to a forest preserve road. The Koolau soil in this area has a grey surface 8 to 10 inches in thickness with a reddish-brown, yellow-mottled layer below.

A 5-ft *M. malabathricum* plant about 20 ft from the *R. tomentosa* thicket was also excavated and the tap root was traced to a depth of 18 inches where water rapidly filled the trench.

A series of *R. tomentosa* plants in the Halii



FIG. 2. *Melastoma malabathricum* excavated in the Kapaa soil series, Wailua Game Refuge. Note the shallow lateral roots and the small tap root.



FIG. 3. Plants of *Rhodomyrtus tomentosa* from the Halii soil series on Kilohana Crater, Kauai. The lateral root of the larger plant was 11 ft long.

soil series were excavated on the northern slopes of Kilohana Crater. These plants had extremely shallow root systems with tap roots turning laterally at about a 4-inch depth and with lateral roots almost at the soil surface (Fig. 3). *R. tomentosa* shrubs in this area were easily pulled up without digging, and tracing of lateral roots was accomplished by pulling. Excavation of such roots was difficult because of long overlapping lateral roots of surrounding plants. One 40-inch plant had a lateral root which arose from the tap root about 2 inches below the soil surface and which was traced at depths of 1 inch or less for 11 ft.

No evidence of root injury was found in *R. tomentosa* plants grown in pots except for an unusual blunting of root tips in the Halii soil. This blunting is best described as a curving and thickening of the root tip which then resembled a miniature chicken's head. Some blackened tips were also found in the Halii soil, but since the concretionary iron-rich surface of the Halii soil was used in these pots it is doubtful that these root abnormalities were due to Al injury.

The only evidence for thicket formation of *R. tomentosa* in this pot study was the presence of a number of buds on the tap root just below the soil surface. Young shoots were observed arising from these buds and often 6 to 10 young shoots were growing simultaneously on one plant. The number of shoots arising from buds increased with time. Bud numbers of single plants ranged from 5 to 30.

Root Development of Leucaena glauca

Root development of *Leucaena glauca* in treated subsoils of the Halii and Kapaa soil series was investigated separately in pots. In both the Kapaa and Halii subsoils root development was usually restricted to the untreated topsoil if subsoils were untreated. The greatest root development in subsoils was produced by P treatments. Treatments in which lime was added in addition to P stimulated root growth more than lime alone. The addition of 1,000 lb of elemental P without lime produced the most root penetration into the subsoils and also the highest plant yields.

Comparative root systems produced by treatments in the Kapaa subsoil are illustrated in Figure 4. Tap roots of *L. glauca* in the P treatments were straight and penetrated to the bottom of the pot. Tap roots of check plants did not develop in the untreated subsoils. The effect of treatment on tap-root penetration and root development in treated Kapaa subsoil ranked as follows: P > lime plus P > lime > check.

Figure 5 shows comparative root systems in Halii subsoils. Roots of check plants in the Halii subsoils penetrated slightly into the subsoil, but total root development in the check was much less than total development in subsoils treated with P and with lime plus P.

Two types of tap-root development with treatment were observed. A long straight tap root was characteristic of P treatment, while a

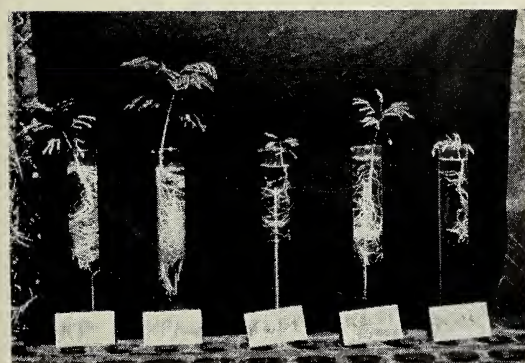


FIG. 4. Plants of *Leucaena glauca* grown in treated subsoils of the Kapaa series. Treatments from left to right are: 500 lb P, 1,000 lb P, 5 tons lime, 5 tons lime plus 1,000 lb P, and check.

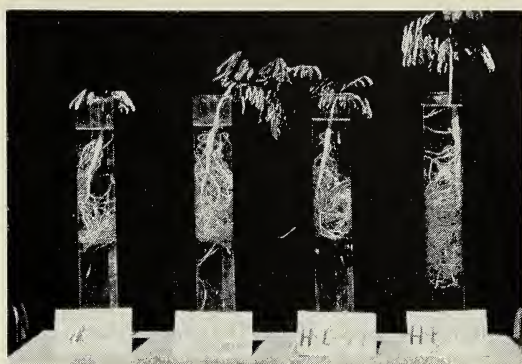


FIG. 5. Plants of *Leucaena glauca* grown in treated subsoils of the Halii series. Treatments from left to right are: check, 5 tons lime plus 1,000 lb P, 5 tons lime, and 1,000 lb P.

branching tap root was characteristic of the lime plus P treatment.

An interesting result of treatments added to Halii subsoils was the number of nodules produced on roots of *L. glauca*. Most nodulation occurred with lime plus P, but lime alone also stimulated nodule formation. Only one nodule was found with P treatment, and no nodules were found in the check.

Staining of Leucaena glauca Root Tips

Hematoxylin staining of cell walls, nuclei, and cytoplasm was evident (Fig. 6*d*). Outer walls of epidermal cells were especially heavily stained (Fig. 6*a, b*), which may indicate a precipitation of aluminum in this region. In P-treated plants two darkly stained areas at the periphery of the stele were observed, which may also represent areas of aluminum precipitation. One of these areas is shown in Figure 6*c*. The cells of the stele appeared to stain more intensely than those of the cortex (Fig. 6*a, b*), but the stelar cells are less highly vacuolated and thus contain more stainable material per unit volume than the cortical cells.

Staining was more intense in roots from the check (Fig. 6*a*) than in roots from lime-treated soils (Fig. 6*b*). Phosphate-treated roots stained more heavily than lime-treated roots. Roots treated with a combination of 5 tons lime plus 1,000 lb P stained more deeply than those treated with lime alone, but in most cases

stained less deeply than those treated with P alone. Staining of nuclei was especially pronounced in the 1,000 lb P treatment.

The results obtained in this study differ from those reported by McLean and Gilbert (1927) for corn and cabbage, and by Wright and Donahue (1953) for barley, in that cells from stelar regions stained readily in all our preparations. Although McLean and Gilbert noted staining of nuclei and cytoplasm, this staining was restricted to the epidermis and outer cortex, and none of the stelar cells were stained. Wright and Donahue found that staining occurred from the epidermis to the outer wall of the endodermis, but that there was very little staining in the stelar region.

DISCUSSION

The importance of the effect of high soil Al on root growth cannot be minimized, but shallow root development in the Hali and Kapaa soil series was not interpreted as resulting from "Al toxicity." High soil Al can cause conditions in the soil which may limit root development, however. From previous work, it is known that Al can interfere with phosphate nutrition of the plant both by precipitation of phosphorus in the soil and possibly by precipitation within the plant. In addition, Al is thought to contribute to the acidity of the soil. If high alumina content of these subsoils is important in limiting root development of plants in bauxitic soils, any decrease in extractable Al and plant Al

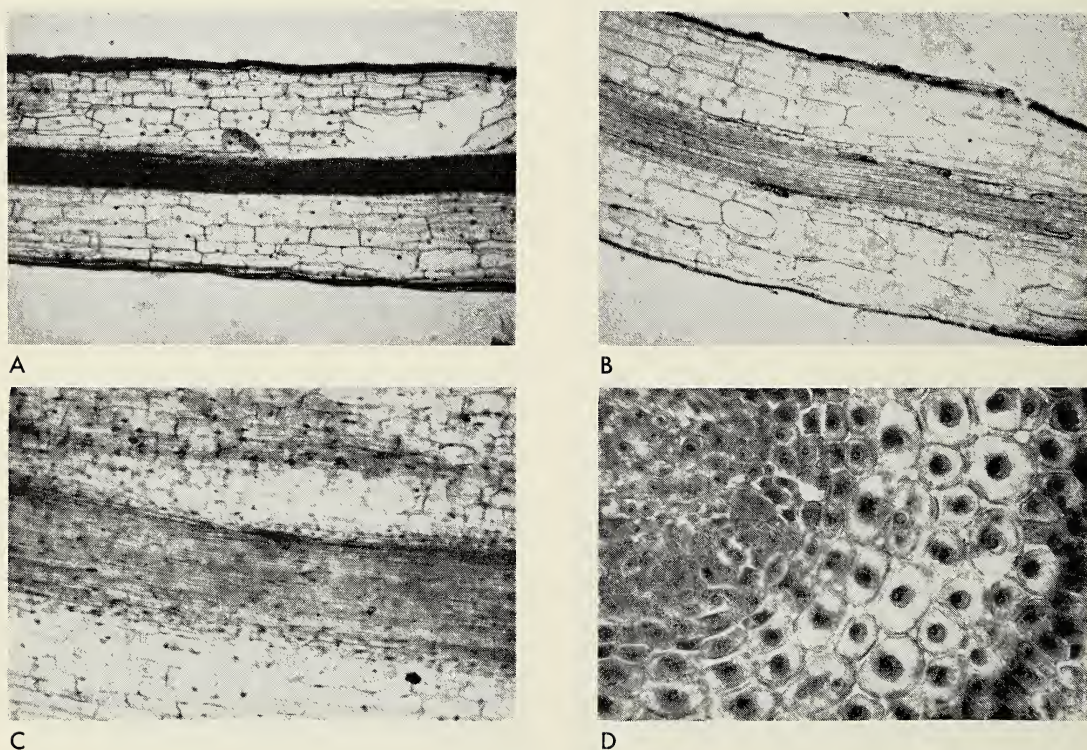


FIG. 6. Photomicrographs of *Leucaena glauca* roots sectioned and stained with hematoxylin. A, Root section from the untreated (check) subsoil of the Kapaa soil series. B, Section from Kapaa subsoil treated with 2.5 tons lime. C, Root from Kapaa subsoil treated with 500 lb P. Note heavily stained area in xylem region. D, Cross-section of root from Kapaa subsoil treated with 5 tons lime plus 1,000 lb P. Note staining of nuclei, cell walls, and cytoplasm.

should result in stimulated root growth. An examination of results of liming treatments shows, however, that although pH was increased and extractable Al and plant Al concentrations were decreased by liming, no marked stimulation of root development or plant growth of *L. glauca* occurred with liming. The increased root development of *L. glauca* in P-treated Hali and Kapaa subsoils in pots is interpreted more as a response to P than a decrease in Al effects. In addition, of course, a mass-action effect may be operating in which active aluminum in the soil is being supplied with enough phosphorus to permit complete precipitation as aluminum phosphate with enough remaining to supply the plant with adequate P.

Deep tap-root development in the Koolau soils was unexpected because of the extremely poorly-drained condition of this soil. Root growth in the wet Koolau soil in pots also appeared normal even though figures for extractable Al were high.

The lack of root damage in plants used in this study was probably related to the evolutionary background of the plants, which seem to thrive in areas of low fertility and high rainfall. Roots of plants sensitive to Al, like rye or barley, would probably be severely injured in these soils. But *Leucaena glauca*, like many other tropical plants, does not respond markedly to lime.

Thicket formation in *R. tomentosa* is probably caused by the large number of adventitious shoots which arise from buds on the tap root just below the soil surface.

Heavy staining of roots with hematoxylin cannot be definitely attributed to Al alone, since iron and other metals may also act as a mordant for hematoxylin. However, since in the present study chemical analysis showed Al to be present in large amounts, much of the staining obtained is attributed to Al. The particularly intense staining of the outer walls of the epidermis, and of two areas in the outer part of the stele, are interpreted as an indication that Al precipitation may have occurred in these areas.

Our results appear to differ significantly from those of McLean and Gilbert (1927) and of Wright and Donahue (1953). The reasons for these differences are not immediately apparent.

In all three studies root sections were stained in hematoxylin without the addition of a mordant, and the staining which occurred was interpreted as an indication that aluminum was already present in the tissues.

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Studies in the Hawaiian Rutaceae, IV New and Critical Species of *Pelea* A. Gray¹

BENJAMIN C. STONE²

THE FOLLOWING NOTES, including descriptions of four proposed new species, are the partial outcome of monographic studies of Hawaiian genera. *Pelea* is a genus confined to the Hawaiian and Marquesan archipelagoes, with all but two of its species endemic to the Hawaiian Islands. There are four relatively natural sections of the genus, characterized primarily by features of the mature fruits and to a lesser extent by leaf arrangement. Systematic treatment of section *Pelea*, which includes the type species, *Pelea clusiaefolia*, is completed. The following notes apply to sections *Apocarpa*, *Megacarpa*, and *Cubicarpa*, as defined by the writer (Stone in Degener, 1962). Related studies have recently appeared or are now in press (Stone 1962a, 1962b, Stone in Degener, 1962). Casual collecting of species of *Pelea* was begun by the author in 1955; in 1958 and 1959 and summer, 1961, intensive field and herbarium studies were carried out. Through the courtesy of the U. S. National Herbarium, Smithsonian Institution, loans of historically important collections were obtained, and I am grateful to Dr. H. R. Fletcher, of the Royal Botanic Gardens, Edinburgh, Dr. George Taylor of the Royal Botanic Gardens, Kew, Dr. J. E. Dandy of the British Museum (Natural History), Dr. Alicia Lourteig of the Museum d'Histoire Naturelle, Paris, Dr. Richard A. Howard of the Arnold Arboretum of Harvard University, and Dr. A. J. Eames of Cornell University for their aid. I am particularly indebted to the former Director of the Bishop Museum, Dr. Alexander Spoehr, Botanist Marie C. Neal, and Curator of Collections E. H. Bryan, Jr., for their generous assistance.

The following comments are arranged by generic section.

¹ The greater part of this work was accomplished at the University of Hawaii and at the U. S. National Herbarium. Manuscript received February 27, 1962.

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SECTION *Apocarpa* STONE

1. *Pelea ovata* St. John & Hume in Lloydia 7: 272, 1944.

P. Forbesii St. John & Hume, l.c. Syn. nov.

Examination of the holotype specimens shows that the pubescence which is found on *Forbes 369.K*, the type of *P. Forbesii*, is not constant, but is found only on one leaf, perhaps from an abnormal cause. It has been noted that leaf-galls of other species, even ordinarily glabrous ones, will often be densely puberulent. Even the new leaves and buds of *P. Forbesii* are found to be glabrous. Since no other character or combination of characters appears to distinguish this from *Pelea ovata*, it is concluded that but one species is represented. Since the description of *P. ovata* calls for glabrous leaves, and since there is no question of priority involved, both descriptions first appearing on the same page of the publication, the name *P. Forbesii* is relegated to synonymy.

Pelea ovata is a vinelike shrub endemic to the island of Kauai.

2. *Pelea hawaiiensis* Wawra in Flora 56:110. 1873.

P. cinerea var. γ Hillebrand, Fl. Haw. Ids. 69, 1888; Rock, Indig. Trees Haw. Ids. 239, 1913 (in part, excluding Oahu plants).

P. cinerea var. *hawaiiensis* (Wawra) Rock in Bot. Gaz. 65:265, 1918.

A tree with smooth light-brown bark, opposite leaves, and generally pubescent innovations; the pubescence of fulvous or reddish hairs, rarely pale; petioles, twigs, and leaves sometimes soon glabrate, commonly with a more or less persistent indument; inflorescences usually densely puberulent, or tomentose, cymose, with generally 3 to 27 flowers, axillary; flowers with deltoid acute thick tomentellous sepals; petals deltoid-

lanceolate, tomentellous, often reddish within; stamens glabrous; ovary densely tawny or golden tomentellous; style hirsutulous; stigma dark maroon, glabrous; capsule commonly 16–34 mm broad, often subtended by the persistent sepals, the carpels with a dense persistent fulvous or reddish pilosity; endocarp firm, thickly pilose with pale hairs.

TYPE: Hawaii: Kawaihae-iuka, in 1862, Wm. Hillebrand (in the Wawra Herbarium, Vienna). A photo shows capsules 27 mm broad.

(a) var. *hawaiiensis*

The typical variety, which is certainly distinct from *Pelea cinerea*, as was stated (in herb.) by the late C. N. Forbes, is nonetheless a southeast counterpart of that species. The distribution of

the typical variety includes Hawaii and Maui. Other varieties, some of them eminently distinct, others only poorly differentiated, are found on Hawaii, Maui, Lanai, and Molokai.

(b) var. *rubra* (Rock) B. C. Stone, comb. nov.

P. cinerea var. *rubra* Rock in Bot. Gaz. 65: 264, 1918.

P. oblongifolia var. β Hillebrand, Fl. Haw. Ids. 65, 1888.

P. cinerea var. δ Rock, Indig. Trees Haw. Ids. 239, 1913.

P. cinerea var. δ Hillebrand, op. cit. 69. (as to Kau specimen).

Hillebrand tells us that this is a glabrous shrub with long rambling branches. The poorly

KEY TO VARIETIES OF *Pelea hawaiiensis*

Capsules mostly 27–34 mm diameter (rarely smaller); inflorescences often few-flowered (3–9).

Leaves puberulent beneath, at least on the costa, at first (and often persistently) uniformly tomentellous to pilose; inflorescence compact, with stout axes, peduncles ca. 2 mm thick, densely tomentellous; capsular pubescence fulvous to brownish-orange. Hawaii.....

.....var. *hawaiiensis*

Leaves glabrous, glossy; inflorescences elongate, the axes slender, peduncle to 1 mm thick, glabrous or nearly so; capsular pubescence reddish. Hawaii.....

.....var. *rubra*

Capsules smaller, mostly 16–22 mm diameter; inflorescences mostly compact and multiflorous with 9–27 flowers, or rarely more open and with fewer flowers.

Blades densely shaggy-pilose beneath, short-lanceolate; branchlets puberulent; inflorescences mostly 3–9-flowered.

Blades cordate at base; tomentum fulvous, the hairs extremely minute. Molokai.....

.....var. *molokaiana*

Blades subcuneate to rounded at base; tomentum brownish or olivaceous, the hairs up to 0.7 mm long. Maui, Lanai.....

.....var. *pilosa*

Blades tomentellous to glabrate beneath, sometimes at last glabrous; inflorescence several- to many-flowered (with up to 27 flowers), or less commonly only 3–7-flowered.

Inflorescences mostly only 3–7-flowered.

Blades cordate or emarginate at base, slightly puberulent on the costa dorsally, elongate and often acuminate. Lanai.....

.....var. *sulfurea*

Blades cuneate at base, glabrate to glabrous beneath, rather broad, ovate. Maui.....

.....var. *Brighamii*

Inflorescences mostly 9–27-flowered.

Blades cordate or subcordate at base, or sometimes merely emarginate; inflorescences about 4–6 cm long.

Blades glabrate beneath; petioles mostly 20–45 mm long. Maui.....

.....var. *Remyana*

Blades puberulent beneath; petioles mostly 7–18 mm long. Maui.....

.....var. *racemiflora*

Blades cuneate or rarely slightly emarginate at base; inflorescences compact, 2–3 cm long; costa puberulent or glabrous dorsally. Hawaii.....

.....var. *Gaudichaudii*

developed capsule of the specimen which he described (with a question mark) as a variety of *Pelea oblongifolia* (a species of sect. *Megacarpa*) misled him; on closer examination, it can be seen that only one follicle is developed, and it is thus difficult to ascertain whether the fruit is apocarpous or syncarpous. However, the tomentum of both the follicle and the endocarp, as well as the leaf venation, suffice to establish the relationship of this plant with *P. hawaiiensis*, rather than with the similar *P. cinerea* of Oahu (which has pubescent endocarp but glabrous follicles), or the greatly different *P. oblongifolia* of Hawaii (with glabrous endocarp and sparsely puberulent syncarpous capsules).

TYPE: Hawaii: North Kona; Huehue, lavabeds, 6 June 1909, *Rock 3565* (Bishop).

Distribution: Kona and Kaū, Hawaii; Olowalu, Maui.

SPECIMENS EXAMINED: Maui: Central ridge of Olowalu valley, 12 May 1920, *Forbes 2345.M.* (Bishop). Hawaii: North Kona, Puuwaawaa, 6 June 1909, *Rock 3561* (Bishop). Kaū, *Hillebrand 251* (Kew), *252* (Kew), without number (Kew). Kaū Desert, 2 August 1911, *Forbes 385.H.* (Bishop).

(c) var. *pilosa* St. John in *Lloydia* 7:272, 1944.

P. cinerea β var. *Hillebrand*, *Fl. Haw. Ids.* 69, 1888 (as to Lanai specimens with pilose blades).

This variety is limited to Lanai and Maui. Hillebrand's description is based mostly on the Lanai specimen, although he cites *Mann & Brigham 371* from Makawao, Maui. This is a misprint for 377; Hillebrand wrote 377 on the label of his own collection as a note citing the Mann and Brigham specimen for comparison; but their specimen is a different variety (var. *Brighamii*). Rock erred in calling his Maui specimens the same, and, after coining the name *sulfurea*, applied it to both the Hillebrand and the Mann and Brigham specimens; var. *sulfurea* is restricted to Lanai. Unfortunately, the type of var. *pilosa* was destroyed at Berlin during World War II.

SPECIMENS EXAMINED: Maui: South slope of Haleakala, March 1920, *Forbes s.n.* (Bishop); Auahi (Auwahi), March 1920, *Forbes 2099.M.*, *2098.M.*, *2097.M.*, *2115.M.*, and *s.n.* (Bishop).

(d) var. *molokaiana* B. C. Stone, var. nov.

Folia base cordata, infra fulvo-pilosa.

HOLOTYPE: Molokai: Ridge below Puu Kolehokole, July 1912, *Forbes 126.Mo.* (Bishop; isotype at US).

DISTRIBUTION: Restricted to Molokai.

The innovations are densely tawny-hirsutulous; blades lance-ovate, rounded or acute at apex, subcordate to cordate at base, up to 8×3.5 cm, with petioles densely hirsutulous, as are the lower surfaces of the blades.

(e) var. *sulfurea* (Rock) B. C. Stone, comb. nov.

P. cinerea var. *sulfurea* Rock in *Bot. Gaz.* 65: 265, 1918.

P. sulfurea (Rock) St. John & Hume in *Lloydia* 7:274, 1944.

TYPE: Lanai: Without locality, July 1870, *Hillebrand* (Kew; isotype, Bishop).

DISTRIBUTION: Restricted to Lanai. Abundant collections are in the Bishop Museum Herbarium.

(f) var. *Brighamii* (St. John) B. C. Stone, comb. nov.

P. Brighamii St. John in *Lloydia* 7:271, 1944 (sub sect. *Cubicarpae*).

TYPE: Maui: Makawao, *Mann & Brigham 377* (Bishop, GH).

DISTRIBUTION: Maui.

Described as a species but, no doubt through a typographic error, misplaced under section *Cubicarpae*. This is the variety that Rock had in mind when he discussed var. *sulfurea* (in *Bot. Gaz.* 65:265, 1918), although he did not typify that variety, but left Hillebrand's original intent as applying to Lanai plants.

A number of specimens have been seen, mostly from Makawao, Olinda, and Olowalu.

(g) var. *Remyana* B. C. Stone, var. nov.

Arbor, innovationibus dense fulvo-hirtellis; foliis maturis supra glabris infra glabris costa media sparse puberulo vel glabrato exceptis, laminis 5–16 cm longis, 2–6.5 cm latis, subanguste ellipticis, apice rotundatis vel emarginatis, base subcordatis vel cordatis (vel emarginatis); inflorescentiis 15–21 (–27–) floriferis; capsulis

densa fulvo-puberulentibus, c. 20 mm diametro; endocarpio hirtello.

HOLOTYPE: Hawaii: Without definite locality, *Jules Rémy* 626 (Paris).

DISTRIBUTION: Known only from Hawaii.

(h) var. *racemiflora* (Rock) St. John in *Lloydia* 7:272, 1944.

P. cinerea var. *racemiflora* Rock, Indig. Trees Haw. Ids. 241, 1913.

TYPE: Maui: Auahi, on aa lava, at about 1500 feet alt., November 1910, *Rock* 8676 (Bishop).

DISTRIBUTION: Maui.

SPECIMEN EXAMINED: Maui: Pakiloi forest, March 1920, *Forbes* 2082.M. (Bishop).

(i) var. *Gaudichaudii* (St. John) B. C. Stone in *Pac. Sci.* 16:369-371, 1962.

P. Gaudichaudii St. John in *Lloydia* 7:272, 1944.

brunelia sandwicensis Gaud. nom. nud. in *Bot. Freycinet Voy. in obs.* 1826.

TYPE: 'Sandwich Islands,' *Gaudichaud* (Paris; fragment at Geneva).

DISTRIBUTION: Hawaii, especially around Kilauea and vicinity.

3. *Pelea makabae* B. C. Stone, sp. nov.

Arbor; innovationibus minute puberulentibus; foliis maturis infra dense cinereis, laminis olivaceis, trichomiis ad 0.1 mm longis, cum squamulis interspersis; petiolis 10-22 mm longis, 1-2 mm crassis, glabrescentibus; laminis anguste ovatis vel ellipticis, rare late lanceolatis, coriaceis, ca. 3.5-12 cm longis, 1.5-5 cm latis, base cuneatis, apice subacutis; inflorescentiis axillaribus, cymosis unifloris (vel trifloris?), axibus cinereis, ad 12 mm longis, binodosis; floris ignotis; sepalis caducis; capsulis 20-24 mm diametro lobis discretis follicularibus glabris punctatis, apice minute mucronulatis; endocarpio glabro.

HOLOTYPE: Oahu: Waianae Mountains, Makaha Valley, near top of ridge, at about 4000 ft. alt., 21 October 1954, *Gordon A. Pearsall* s.n. (Bishop).

A characteristic species closely allied to and simulating *P. cinerea*, but with glabrous endocarp; similar also to *P. cinereops* but with glab-

rous ovary. The disk may however be slightly puberulent.

The cinereous indument is extremely fine, composed of waxy scales intermingled with hairs less than 0.1 mm long, obscuring the densely glandular-punctate surface of the lamina. The indument tends to persist on the younger petioles and stems, also. The leaf margins are usually very slightly inrolled; the lateral nerves are ascending, parallel, and united by a sinuate marginal nerve 1-8 mm or more in from the edge.

SECTION *Megacarpa* STONE

4. *Pelea Balloui* Rock, Indig. Trees Haw. Ids. 228, 1913.

P. ukuleleensis St. John (as to flowering branch of type sheet), in *Lloydia* 7:267, 1944. Syn. nov.

The type specimen of *P. ukuleleensis* is a mixture of two species: the flowering material is from a plant of *P. Balloui*; fruits of *P. clusiae-folia* are mounted on the same sheet. Hence the species is based on mixed material, of which both elements already bear valid names, and the name *ukuleleensis* is relegated to synonymy.

The type of *P. Balloui* is: Maui: Haleakala, trail from Ukulele to Waikamoi Gulch at ca. 5000 ft. alt., 25 October 1910, *Rock & von Tempisky* 8609 (Bishop).

The type sheet of *P. ukuleleensis* is: Maui: Ukulele, July 1919, *Forbes* 749.M. (Bishop).

4. *Pelea Hiiakae* B. C. Stone, sp. nov.

Arbuscula; innovationibus minute puberulentibus glabratibus; foliis, petiolis, ramulisque glabris; petiolis filiformibus 9-21 mm longis, 1 mm crassis; laminis ellipticis base cuneatis vel subrotundatis apice obtusis vel rotundatis, 3.5-6.5 cm longis et 2-3.5 cm latis, glabris, costa media anguste dorsaliter salientis brunneis, nervis lateralibus paralleliter ascendentibus, cum nervio sublineare a margine distans 1 mm coalitis; inflorescentiis axillaribus 2-3-nodosis, ad 3.5 cm longis in fructu, axibus glabris, pedunculis 3-8 mm longis, in crassitudine petiolo aequis, pedicellis claviformibus, sub calyce expansis; cymis unifloriferis; floris ignotis; capsulis ca. 25 mm diametro profunde ($\frac{2}{3}$ - $\frac{3}{4}$) lobatis lobis

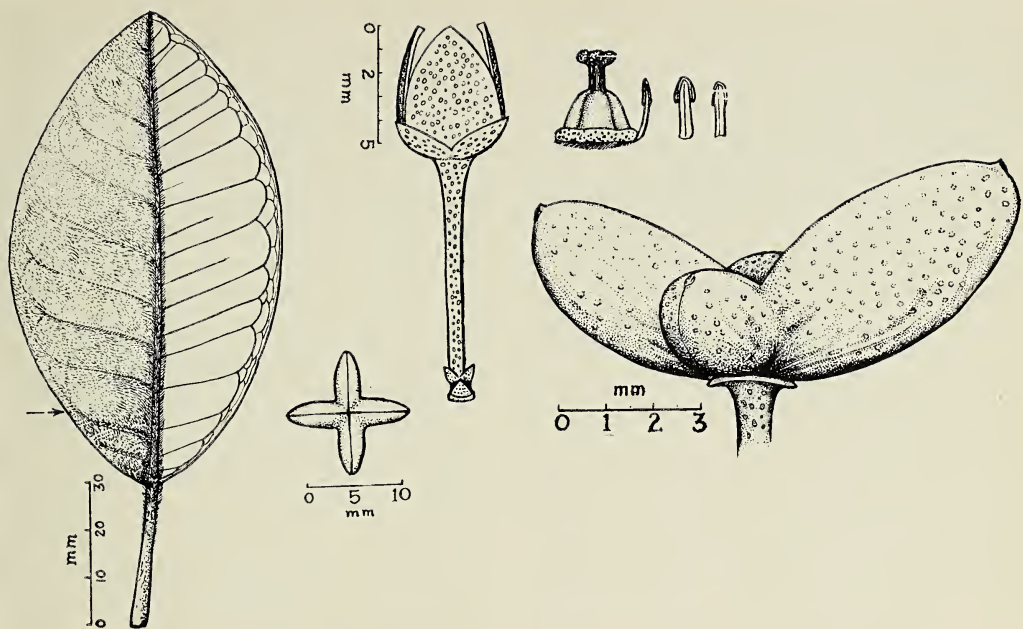


FIG. 1. *Pelea kauaiensis* H. Mann. Holotype specimen, Mann & Brigham, Cornell Univ. Herb. A leaf, showing pubescence and venation of lower surface; a flower (the entire 1-flowered inflorescence), showing the glandular-punctate appearance; floral parts; immature capsule in side view; and reconstructed conjectural top view of a mature capsule.

rotatis; exocarpiis ad basim sparse puberulentibus glabrescentibus; endocarpio sparse hirtello trichomiis ad suturas dorsales aggregatis; lobis diseminatis; seminis ovoideis, ca. 5–6 mm longis; testa crustacea nigra nitida.

HOLOTYPE: Oahu: Koolau Range, Kipapa Gulch, Waipio, on southerly ridge in woods at 1800 ft. alt., 16 October 1932, Edward Y. Hosaka 809 (Bishop).

This species seems to be related to *Pelea descendens* St. John, which however is characterized by smaller capsules 13–17 mm in diameter, with glabrous exocarp and quite glabrous endocarp. *Pelea Hiiakae* is also related to *P. Wawraeana* Rock, which differs in that the pubescence of the endocarp is restricted to the innermost part of the sutures (and may sometimes be lacking), and in the more compact, shorter, multi-flowered pubescent inflorescences.

The species is named in honor of Hiiaka, youngest sister of the goddess Pele, heroine of the tales of Pele and Hiiaka.

It must be noted that this specific name was first applied to certain specimens from the island

of Kauai which were thought to represent an undescribed species (Stone 1626, Faurie 225, and Lydgate s.n.). Since doubt remains as to the fruiting state of these plants and their specific distinctness from *Pelea anisata*, they must remain undescribed. The name *Pelea Hiiakae* must now be borne by the Oahu plant described above, as this is the first publication of the name. Should the Kauai plants ultimately prove distinct, another name will be given to the species.

5. *Pelea kauaiensis* H. Mann Jr. in Proc. Boston Soc. Nat. Hist. 10:313, 1866.

Fig. 1

A small tree to 5 m high, with opposite leaves; innovations minutely but densely tawny-puberulent, but the branches quickly glabrate, at the 3rd or 4th node quite glabrous. Leaves distinctly petiolate, petioles 12–30 mm long, flattened ventrally and narrowly and shallowly channelled and nearly glabrous or with a few scattered minute trichomes at the margins; the rounded dorsal surface especially near the distal

end hirsute with trichomes 0.8–1.0 mm long; but the whole petiole glabrate and ultimately glabrous. Blades 5–10 cm long, 3–6 cm broad, elliptic, usually rounded at base, broadly subacute at apex or there minutely retuse, ventrally glabrous even in bud, densely villous beneath all over the dorsal surface and densely hirsute along the costa, with pale stramineous trichomes ca. 1 mm long, the indument more or less permanent; costa raised and rounded dorsally; lateral nerves 8–14 per side, nearly straight and parallel, the connecting marginal nerve deeply arched, with several minor veinlets intervening between it and the margin; marginal nerve ca. 2–8 mm from the edge. Inflorescence a highly reduced cyme with usually 1 or rarely 2 to 3 flowers, axillary among the leaves; peduncle and pedicel sparsely and minutely puberulent in flower, later subglabrate; peduncle reduced to a slight projection no higher than the 2 or 4 bractlets it bears, and hidden by them; pedicel ca. 5 mm long, 0.3–0.4 mm thick, slightly flaring at calyx to a breadth of 0.7–0.9 mm, with bractlets tightly appressed at base of pedicel on the obsolete peduncle; bractlets deltoid, ca. 0.3–0.4 mm long, opposite, decussate; pedicels and perianth segments copiously opaque-punctate. Pistillate flowers ca. 3 mm high, sepals broadly ovate with rounded summit and sharp apex, 1.3 mm long, 1.5 mm broad, glabrous except for the minutely ciliolate margins. Petals glabrous, broadly ovate, acute, 2–4 mm long, ca. 1.7 mm broad. Stamens sterile, all shorter than the style, in 2 subequal quartets, the shorter quartet just under 1 mm long, the longer quartet bare more than 1 mm long. Ovary 4-lobed, glabrous, ca. 1 mm high, 1.3 mm broad, on a glabrous shallow somewhat reddish-speckled disk, the style 0.5 mm high, stigma 4-lobed, ca. 0.7 mm broad, the lobes dark purplish and minutely papillate. Staminate flowers unknown. Immature capsule nearly 10 mm diameter, the lobes (some abortive) still more or less ascending, 5 mm long, deeply parted ($\frac{4}{5}$ – $\frac{5}{6}$), sepals caducous; exocarp glabrous, copiously glandular-punctate; endocarp glabrous; lobes 2-seeded.

TYPE: Kauai: Waimea, 2000–3000 ft. alt., Mann & Brigham s.n. (Cornell).

DISTRIBUTION: Kauai.

Only one further collection of this species is known; it is from the general area of the type

locality (Waimea, Kauai) and was discovered by Otto Degener. Unfortunately, it is a sterile specimen.

This species has been consistently misinterpreted since its first description. Hillebrand (1888) described under the name *Pelea kauaiensis* a species superficially similar to that which Mann had actually described, but clearly distinct; Hillebrand's material was correctly segregated by Rock (1918) under the name *Pelea recurvata* Rock. In 1897 Heller described *Pelea cruciata*, which was however considered by later authors, such as Rock, to be a synonym of *Pelea kauaiensis* Mann. Such was not the case; Heller's species was justly distinguished, and is quite distinct from both *Pelea kauaiensis* or *Pelea recurvata*. Skottsberg (1944) noted the discrepancies between descriptions and specimens of these three entities, and published in tabular form some of their differences. Upon comparing type specimens of the three species it becomes quite apparent that they are distinct. The above extended description of *Pelea kauaiensis* is based on the original material, and should serve finally to clarify this least understood member of a trio of superficially similar species.

Pelea kauaiensis may be quickly distinguished from the two other species formerly confused with it as follows:

1. Endocarp glabrous.
 2. Blades permanently pilose beneath; capsule lobes ascending or rotate; capsules 10–? (perhaps 20) mm diameter; inflorescence reduced, 1–3-flowered.....*kauaiensis*
 2. Blades ultimately slightly glabrescent; capsule lobes recurved; capsules 21–23 mm diameter; inflorescence stout, 3–9-flowered.....*recurvata*
1. Endocarp pubescent; blades densely puberulent.....*cruciata*

Mann's original description indicated the name as *kawaiensis*; since, however, the Latin *v* is more commonly spelled out either as a true *v* or as *u* in modern usage, and since the *u* is essential to the meaning as well as the pronunciation of the name, it is thought best to retain with Hillebrand the name of the island in its correct form, as *kauaiensis*. See art. 73, note 6,

of the 1961 International Code of Botanical Nomenclature.

Little need be added to the descriptions of *P. recurvata* and *P. cruciata*, but it should be mentioned that Skottsberg 2865, commented upon by Skottsberg (1944) as *P. cruciata*, is actually a specimen of *P. recurvata*, as the endocarp is quite glabrous.

6. *Pelea Lakae* B. C. Stone, sp. nov.

Arbor ad 5 m alta, ramis divaricatis, trunco ad 5–10 cm diametro, innovationibus dense hirsutulis, trichomiis pallide albobrunneis adpressis ad 1 mm longis; petiolis ramulisque glabris; petiolis 10–65 mm longis, 1.5–3 mm crassis; laminis ellipticis vel subovatis vel subobovatis, coriaceis, 4–25 cm longis, 2.5–11 cm latis, base cuneatis vel obtusis, apice subacutis, obtusis vel subrotundatis, supra glabris, infra puberulentibus in pagine juvente glabrescentibus, costa media salientis stramineis vel brunneis puberulentis (trichomiis cum squamulis glaucis interspersis), nerviis lateralibus curvate ascendentibus in extremis cum nervo marginale arcuato 2–10 mm intra margine coalitis, reticulis venulosis minoribus intervenantibus; inflorescentiis axillaribus cymosis, cymis ad 2 cm longis axibus puberulentibus glabris, 2–4-nodosis, 3–5-floriferis, pedunculis 2–7 mm longis pedicellis ca. 3 mm longis; floris ignotis; bracteis deltoideis extus puberulentibus; capsulis maturis 22–32 mm diametro profunde ($\frac{3}{4}$) lobatis lobis recurvatis pre- et postdehiscutionem et paullo reflexis, uni- vel diseminatis, base 8 mm altis, lateraliter compressis, apicem versus angustatis subfalcatis; exocarpio minutè denseque puberulento non-ruguloso; endocarpio glabro in suturam basem centralem excepto, trichomiis paucis aggregatis; seminis ovoideis, 5–6 mm longis, testa crustacea nigra nitida.

HOLOTYPE: Oahu: Koolau Range, Pupukea, at about 2000 ft. alt., at edge of small boggy region, 17 September 1961, B. C. Stone & A. K. Chock 3655 (Bishop; duplicates to be distributed).

A species reminiscent of *Pelea recurvata* of Kauai, but with a puberulent rather than glabrous ovary, and a few hairs clustered near the innermost angles of each suture on the endocarp.

The specific name honors Laka, goddess of the hula.

7. *Pelea Lobiauana* B. C. Stone, sp. nov.

Fig. 2

Arbuscula? ramis virgatis elongatis, innovationibus ramulis petiolisque dense tomentellis, trichomiis stramineis val pallide brunneis ca. 0.8–0.9 mm longis; foliis maturis glabris, juvenilis tomentellis; petiolis 20–30 mm longis, glabrescentibus, supra canaliculatis glabris; laminis ellipticis coriaceis 7–15 cm longis 3.5–7 cm latis base apiceque rotundatis vel paullo emarginatis, marginibus paullo revolutis, costa media prominente, nervis lateralis 5–9 (–12) per latere unico, cum nervo marginale continuo vel paullo arcuato intra margine 1–2 (–5) mm coalitis; inflorescentiis cymosis (3–) 5–7-floriferis longe-pedunculatis tomentellis, pedunculis 12–38 mm longis ad nodo primo, 1–2-nodosis, bracteis oppositis lanceolatis 1.5–2.5 mm longis concavis; axibus majoribus 5–14 mm longis; pedicellis 2–5 mm longis; floris masculis pro genere magnis sepalis ad 5.5–6 mm longis et ca. 4.5 mm latis, extus hirsutulo-ciliolulatis intus

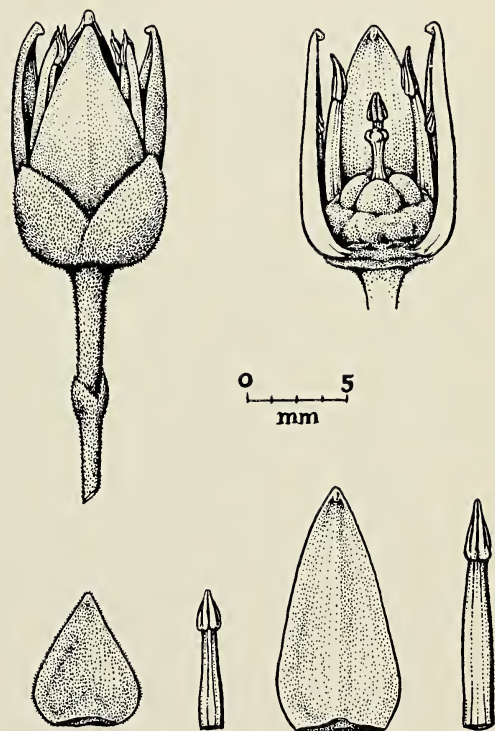


FIG. 2. *Pelea Lobiauana* Stone. Staminate flowers and floral parts of Degener 23984.

glabris, deltoideis, 7–9-nervatis; petalis toto glabris sparse obscure punctatis ovato-lanceolatis ca. 11 mm longis et 5 mm latis apice intus unguiculatis; staminibus fertilibus 8, (4 ad 10 mm longis, 4 ad 7.5 mm longis, antheris 1.7–1.8 mm longis, filamentis ligulatis ca. 1 mm latis); ovario glabro ca. 2 mm alto, disco glabro ca. 1 mm alto; stylo ca. 2 mm longo, stigma ca. 1.4 mm lato lobis rufidis minute papillatis cruciatis; floris foemeneis minoris sepalis ca. 3.5 mm longis et 3 mm latis, petalis ca. 7–8 mm longis et 3.5 mm latis, staminibus sterilibus ca. 2 mm longis subaequantibus; ovario discoque glabro, stylo glabro ca. 4 mm longo; capsulis quadrilobatis, glabris, ad 20–25 mm diametro, endocarpio glabro.

HOLOTYPE: Kauai: Kokee, August 1924, *Degener* 8586 (Bishop; duplicates at Cath, NY).

DISTRIBUTION: Kauai, in the Waimea highlands.

SPECIMENS EXAMINED: Kauai: Near Lehua-makanoe Bog, 18 September 1955, *Degener*, *Hansen & Hanner* 23984 (Bishop; staminate fls.). Kaholuamano, October 1895, *Heller* 2869 (formerly determined as *P. resiniflora*) (GH, EDINB, US). Halemano, 14 February 1909, *Rock* 2294 (A). Waialeale, October 1911, *Rock* (A). Kaholuamano, September 1909, *Rock* 5551 (A, Bishop), 5552 (GH, Bishop).

This is by no means a complete citation of specimens; more are extant, particularly in the Bishop Museum, but many lack data, particularly localities and collectors' numbers. Most of these specimens had been determined as *Pelea macropus* Hillebr., which however is quite distinct in having puberulent ovaries (and hence capsules) and clavoid pedicels. Because of this interpretation, this species has consistently been mistaken for *P. macropus*, and this error has tended to obscure knowledge of both of them. The glabrous endocarp and rotate capsular lobes place *P. Lobiauana* in a group with *P. oblanceolata* St. John (of Hawaii), *P. manukaensis* St. John (of Hawaii), and *P. pseudoanisata* Rock (of Hawaii).

The specific name honors Prince Lohiau of Kauai, hero of the tales of Pele and Hiiaka, and one of the memorable characters of Hawaiian mythology.

8. *Pelea macropus* Hillebrand, Fl. Haw. Ids. 65, 1888.

P. acutivalvata Léveillé in Fedde Repert. Sp. Nov. 10:153, 1911.

Innovations minutely and closely pale cinereous-puberulent, hairs appressed, ca. 0.2 mm long; branchlets at youngest nodes cinereous but soon glabrate; leaves glabrous ventrally, at first minutely cinereous dorsally (mostly on the costa), but soon glabrate, the older leaves mostly quite glabrous; petioles soon glabrate. Leaves opposite, the petioles mostly 9–15 mm long; blades thinly coriaceous, rounded or emarginate at apex, contracted and subcuneate at base (the margins sometimes slightly revolute); costa ventrally pale, shallow-sulcate; dorsally pale and prominent with a rather sparse and minute ephemeral puberulence; lateral nerves at right angles to costa or slightly ascending, about 7–9 per side, conspicuous, prominulent on both surfaces, connected at a distance of 2–10 mm from the margin by a moderately to deeply arcuate marginal nerve, with several sets of intervening meshes. Inflorescences small, axillary or ramuline, mostly 1–3-flowered, the peduncle very short, about 1–5 mm long, bibracteolate at apex, puberulent, the bractlets deltoid, rounded, 0.5 mm long, puberulent; axes minutely cinereous, short (to 5 mm) in flower, somewhat elongated in fruit; pedicels 2–5 mm long, flared at base of calyx and clavoid, bibracteolate, cinereous; pistillate flowers with broadly deltoid sepals about 1.5 mm long and 1.7 mm broad, minutely puberulent externally; petals about 2.5 mm long and 1.7 mm broad, with a faint close puberulence of few minute hairs along the midregion, glabrous within; rudimentary stamens glabrous, less than 1 mm long; disk reddish, glabrous, shallow, ca. 1.7 mm broad; ovary puberulent, ca. 1 mm high and 1 mm broad; style glabrous, ca. 1.6–1.7 mm long (including stigma), stigma lobes red, each 0.25 mm long, minutely papillate, obovoid. Capsules 25–35 mm diameter, about 9 mm high, sparsely appressed-puberulent (especially near the base), the lobes deeply separated ($\frac{5}{6}$), somewhat acuminate and laterally compressed, often unequally developed; endocarp glabrous, cartilaginous; seeds 5–6 mm long, ovoid, the testa crustaceous, blackish.

HOLOTYPE: Kauai: Waimea, *Knulsen* 189 (Berlin; now destroyed).

DISTRIBUTION: Kauai.

SPECIMENS EXAMINED: Kauai: "Robinson's summer house," February 1910, *Faurie* 172 (type of *P. acutivalvata*; type at Edinburgh; isotype at A). Waimea, Kaholuamano, October 1895, Heller 2870 (BM, K. Paris, US).

The description given above sufficiently distinguishes *Pelea macropus* from the newly described *P. Lohiauana*.

SECTION *Cubicarpa* STONE

9. *Pelea peduncularis* Lévillé in Fedde Repert. Sp. Nov. 10:443, 1912.

Fig. 3

P. sandwicensis var. β sensu Hillebrand, Fl. Haw. Ids. 66, 1888 (not *P. sandwicensis* [Hook. f. & Arn.] Gray).

P. sandwicensis var. *macrocarpa* Hillebr. ex Rock in Bot. Gaz. 65:265, 1918.

P. nodosa Lévillé in Fedde Repert. Sp. Nov. 10:443, 1912.

P. grandipetala Lévillé l.c. (in part; specimen typicum mixtum; in part *P. honoluluensis*). Syn. nov.

P. singuliflora Lévillé l.c. (in part; see *P. Wawraeana*). Syn. nov.

P. Rockii St. John in Lloydia 7:271, 1944. Syn. nov.

A small or sometimes shrubby tree, the innovations finely scurfy and somewhat sparsely cinereous-puberulent; trichomes soon caducous, the mature branchlets and leaves glabrous, or the petioles sometimes puberulent then glabrate. Leaves petiolate, opposite; petioles 13–40 mm long, lenticellate in age especially at the extremities; blades coriaceous, elliptic, rounded to slightly emarginate at apex and at base, mostly 3–18 cm long and 2–11 cm broad (commonly $5-9 \times 3-6$ cm), darker above, the margin near the base usually tightly revolute; midrib above sulcate, raised beneath, often reddish or purplish; major lateral nerves mostly about 7–10 per side, united distally by a slightly sinuate marginal nerve close to (about 1–5 mm from) the margin. Inflorescence a pedunculate usually 5–21-flowered minutely cinereous glabrate cyme often

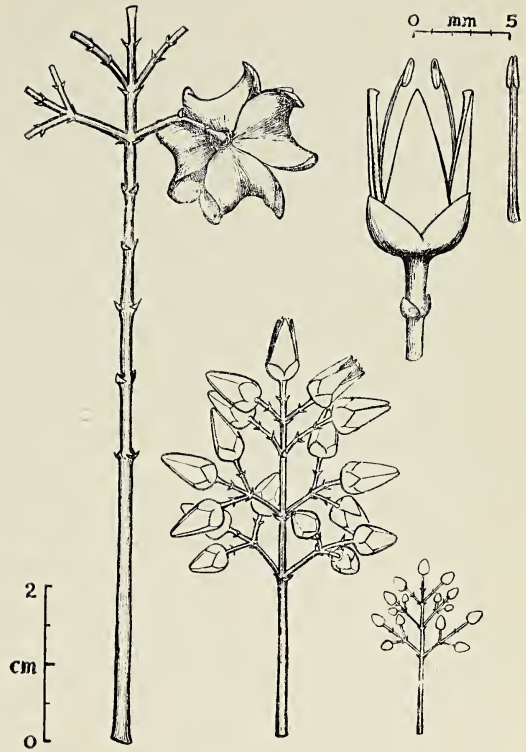


FIG. 3. *Pelea peduncularis* Lév. Inflorescences; at left, a long inflorescence with a dehiscent capsule, from *Faurie* 189 (isotype); at right, inflorescences in flower and in bud from *Rémy* 621, with enlarged view of one staminate flower.

longer than the adjacent petiole, the peduncle up to 4 cm long and with as many as 8 nodes, but usually about 3–4-nodose, stout (1–2 mm thick), the pedicels short and stout, 3–4 mm long, the bractlets lanceolate, the upper ones deltoid, minutely ciliolate and sparsely puberulent, 1–3 mm long; pistillate flowers with sparsely scurfy-puberulent deltoid-ovate sepals about 2 mm long and 1.8 mm broad, lanceolate-ovate glabrous punctate petals about 5 mm long, reduced sterile stamens barely higher than the glabrous 4-lobed ovary, the disk glabrous, the style filiform reddish about 2 mm long, the stigmas 0.5 mm long, slightly clavate and minutely papillate, rotate. Staminate flowers similar but larger, the petals about 7 mm long, the gynoecium much reduced, the fertile stamens longer, in 2 subequal quartets, the longer stamens about 8 mm long. Capsules mostly about

20–25 mm broad and 10 mm high, quadrate or slightly lobed (less than or barely halfway), the exocarp glabrous, punctate, mostly dark green or tinged with dull reddish-purple; endocarp pale and glabrous; seeds mostly 2 per cell; carpels after dehiscence reflexed in age, the axis persistent only at the extreme base.

TYPE: Oahu: Koolau Range, Kalihi, October 1909, *Faurie* 189 (Edinburgh; isotype at Paris).

DISTRIBUTION: Restricted to Oahu; found on both the Waianae and Koolau mountain ranges.

This common Oahu species has been misinterpreted since it was first described. This is not surprising, however, since the confusion involved with the identity of the true *Pelea sandwicensis* (H. & A.) Gray had obscured the concept greatly, and since Léveillé himself did nothing to clarify the species, and presumably did not realize that the other "species" so briefly and inadequately described by him were either the same or mixtures (the type specimens often being composed of branchlets clearly from two or three different species). In addition, some rather clearly defined varieties of the species occur in particular areas of Oahu, and some of these have been described as distinct species. Dozens of collections from various localities both in the eastern and western mountain ranges are known. A few representative specimens are cited here; full citation of specimens will be presented in the forthcoming monographic treatment.

SPECIMENS EXAMINED: Oahu: Koolau Range: Pupukea, January 1927, *MacDaniels* 547 (Bishop); February 1928, *Degener & Shear* 8580 (NY, Catholic, US). Kalihi, October 1909, *Faurie* 190 (BM). Konahuanui, *Faurie* 194 (BM, isoleotype of *Pelea singuliflora*). Manoa-Pauoa hills, April 1861, *Hillebrand* 237 (Kew). Nuuanu,

May 1861, *Hillebrand* 238 (Kew). Nuuanu-Kalihi ridge, August 1922, *Skottsberg* 173 (Goth, Kew); Niu, *Hillebrand* 1797 (US, isotype of *Pelea molokaiensis* β var. Hbd.). Waianae Mountains: Puu Kaala, *Mann & Brigham* 600 (Cornell, Kew). Makaha Valley, Feb. 1909, *Forbes* (Bishop). Puu Kanehoa, May 1960, *Stone* 3268 (Bishop, Goth, Kew, Leiden, US). Without locality: *Mann & Brigham* 208, in part (Cornell). *Rémy* 621 (Paris, 3 sheets).

(a) var. *peduncularis*

Fig. 3

Found mostly along the southern stretches of the Koolau Range, from Punaluu down through Waialae and Niu valleys. The typical variety, easily confused with *Pelea oahuensis* Lévl. and sometimes with *Pelea Wawraeana* Rock, but differing in many respects from both; from the former in the larger and flatter capsules, the more ample and stouter cymes, and generally larger vegetative parts, and the larger reddish (not yellowish) flowers; and from the latter in the larger capsules with glabrous endocarp, and mostly glabrous petioles and branchlets as well as cymes.

(b) var. *niuensis* (St. John) B. C. Stone, comb. nov.

Pelea niuensis St. John in *Lloydia* 7:272, 1944.

Branchlets glabrate; petioles glabrate; blades narrowly elliptic or oblong-elliptic, glabrous, 6–12 cm long and 2–5 cm broad; inflorescences commonly 7–9-flowered, glabrous; capsules nearly quadrate when fresh, slightly lobate when dry, 21–25 mm broad and about half as high, glabrous; endocarp glabrous.

KEY TO VARIETIES OF *Pelea peduncularis*

1. Capsules slightly lobed (up to halfway), green, usually dull, sometimes reddish; blades elliptic to elliptico-oblong.
 2. Leaves opposite.
 3. Blades very narrowly oblong-elliptic.....var. *niuensis*
 3. Blades elliptic to broadly oblong-elliptic.
 4. Cymes mostly 7–21-flowered.....var. *peduncularis*
 4. Cymes mostly 3–7-flowered.....var. *pauciflora*
 2. Leaves whorled in fours.....var. *paloloensis*
1. Capsules unlobed, quadrate, dark glossy green.....var. *quadrata*

HOLOTYPE: Oahu: Koolau Range; Niu, October 1940, *St. John 20111* (Bishop).

DISTRIBUTION: Endemic to the southeastern-most part of the Koolau Range.

This variety differs from the typical *P. peduncularis* only in the much narrower leaves and perhaps slightly fewer-flowered cymes.

SPECIMEN EXAMINED: Oahu: Northeast slope of Puu Kumakalii, April 1936, *Degener, Tam, Takamoto & Martinez 10579* (Bishop, Catholic, NY).

(c) var. *pauciflora* (St. John) B. C. Stone, comb. nov.

Pelea Rockii var. *pauciflora* St. John in *Lloydia* 7:271, 1944.

Cymes mostly 3–7-flowered.

HOLOTYPE: Oahu: Koolau Range; Kaukonahua Gulch, Wahiawa, May 1909, *Rock 3046* (Bishop).

DISTRIBUTION: Known only from the type locality.

A poorly defined variety which may be only an anomalous form of the species.

(d) var. *paloloensis* (St. John) B. C. Stone, comb. nov.

Pelea paloloensis St. John in *Lloydia* 7:271, 1944.

Leaves whorled in fours at the nodes.

HOLOTYPE: Oahu: Koolau Range; Palolo, Waialae-iki, Jan. 1917, *Forbes 2404.O.* (Bishop).

DISTRIBUTION: Known only from the type locality.

The variety, which probably is nothing more than an anomalous form, is an example of the occasional exception to the common taxonomic criterion for distinguishing species which are members of the section *Pelea*, with ordinarily whorled leaves, and the other sections, with generally opposite leaves.

(e) var. *quadrata* B. C. Stone, var. nov.

Fig. 4

Capsulis elobatis quadratis fere ca. 25 mm latis.

HOLOTYPE: Oahu: Waianae Mountains; Puu Hapapa, August 1932, *Degener 8521* (Bishop).

DISTRIBUTION: Known from the northern end of both ranges of Oahu.

A characteristic variety, found both in the northern Waianae mountains and in the northern Koolau Range (as for instance around Pupukea), sometimes occurring in company with the typical variety.

10. *Pelea olowaluensis* St. John in *Lloydia* 7:266, 1944.

A tree up to 3 m high, the branchlets at first puberulent; leaves opposite; petioles glabrous; blades 2.8–8 cm long, oval, subcoriaceous, glabrous; cymes mostly 3-flowered, glabrous, the peduncle ca. 9 mm long; capsules 16–20 mm broad, flattened, lobed halfway or less, glabrous; endocarp glabrous.

HOLOTYPE: Maui: Olowalu Valley, on the central ridge, May 1920, *Forbes 2326.M.* (Bishop).

DISTRIBUTION: West and East Maui.

SPECIMEN EXAMINED: West Maui: Mauna Huuma, May 1910, *Forbes & Cooke 22.M.* (Bishop).

This species is closely allied to *Pelea peduncularis* of Oahu and falls properly into section *Cubicarpa*. The characteristically revolute basal leaf-margins are especially noticeable. When fresh the capsules might perhaps be unlobed or barely notched. The disjunction of the two collections would imply that the species is, or was, fairly widespread on Maui.

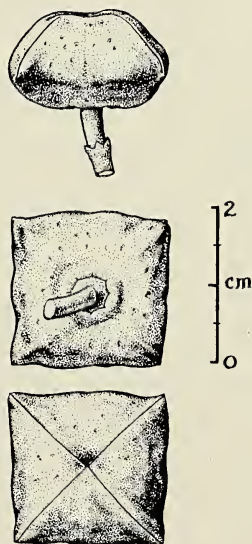


FIG. 4. *Pelea peduncularis* var. *quadrata* Stone. Three views of a capsule in the fresh state, from Stone 2832 (Pupukea, Oahu).

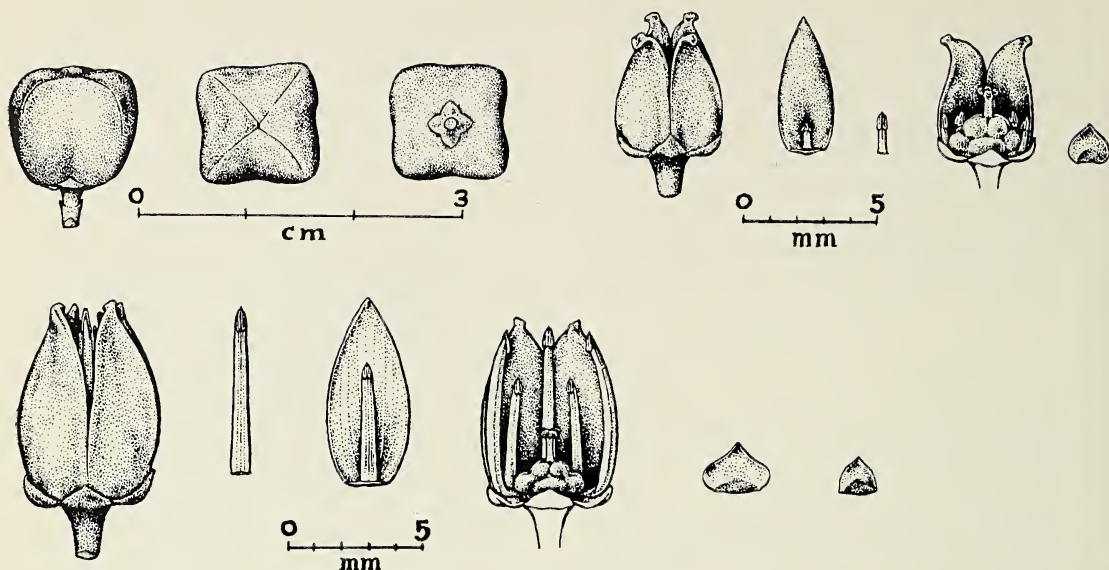


FIG. 5. *Pelea oahuensis* Lévl. emend. Stone. Neotype, Stone 3282. Above, capsules and pistillate flowers; below, staminate flowers.

11. *Pelea oahuensis* Lévillé in Fedde, Repert. Sp. Nov. 10:442, 1912, emend. B. C. Stone.

Figs. 5, 6

A small to middle-size tree, pungent of anise, with glabrous reddish branchlets and opposite leaves; innovations scurfy, the waxy white ephemeral scales mostly concealing an extremely minute sparse puberulence of white hairs usually less than 0.2 mm long, ephemeral also, the older leaves and branchlets glabrous except for a few rare hairs persisting in the axils or on the dorsal midrib near the base; leaves petiolate, the petioles mostly 6–20 mm long, reddish in age, glabrous, flattened ventrally, lenticellate; blades thin coriaceous, mostly (3)–4–12 cm long and 2.5–7 cm broad, glabrous and moderately veiny, darker above, moderately shining, mostly elliptico-obovate, rounded to slightly emarginate at both ends, the costa pale and shallowly canaliculate toward the base ventrally, beyond prominent, beneath raised and reddish; lateral main nerves slightly curvate-ascendent, joined marginally by a lightly arched or nearly straight nerve about 1–5 (–9) mm from the edge. Inflorescence cymose, mostly 3–5-flowered (rarely with 7

flowers), rather short (less than 2 cm long), on short glabrous greenish sometimes scurfy peduncles 3–4 mm long, bibracteolate at apex (the bracteoles minute, deltoid, minutely puberulent or glabrous); axes about 2–3 mm long, similar to peduncles; pedicels about 3 mm long, bibracteolate near the middle or above; flowers functionally staminate or functionally pistillate, or perfect, frequently with both staminate and perfect flowers on the same plant; pistillate flowers greenish, petals yellowish-green; sepals deltoid-ovate, about 1.8×1.8 mm, the margins minutely ciliolulate, otherwise glabrous; petals 4.5–5.5 mm long and 2 mm broad, glabrous; stamens rudimentary, about 1 mm long (sometimes in two slightly unequal quartets); ovary and disk glabrous, punctate, the disk about 2.8 mm broad and nearly 1 mm high, the ovary about 2 mm broad and 1 mm high; style slender, glabrous, about 2 mm long including the 4-lobed stigma; staminate and perfect flowers similar but the stamens greatly elongated, the longer quarter as long as the petals; petals slightly longer than those in pistillate flowers, and the ovary and disk greatly reduced, the style short, only 1 mm long. Capsules subcuboid, 10–14 mm broad, about 9 mm high, unlobed or nearly so,

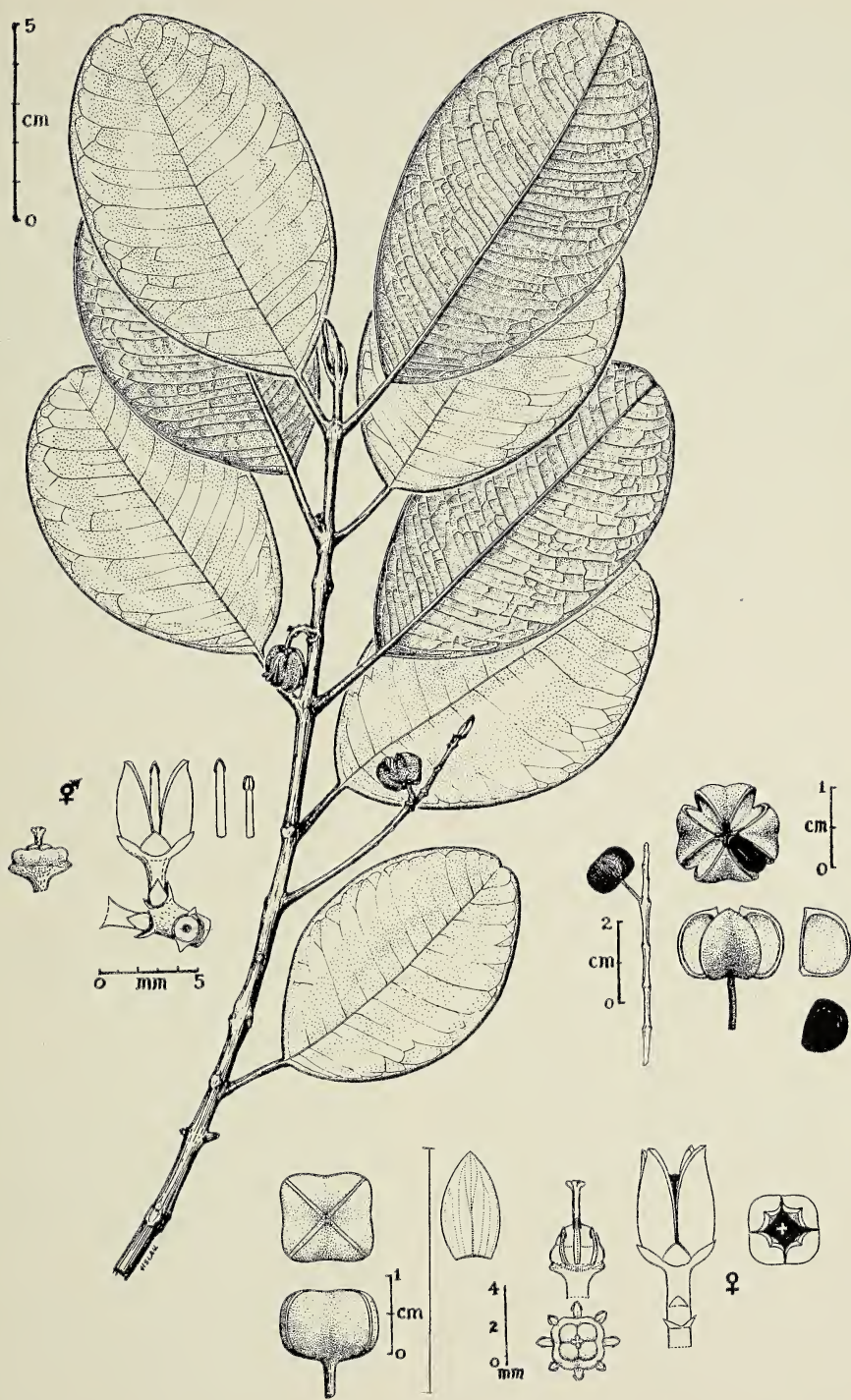


FIG. 6. *Pelea oahuensis* Lévl. emend. Stone. Habit of fruiting specimen, from Stone 2805 (Pupukea, Oahu). At left, perfect flower from Lane 243 (Pupukea). At right, above, capsules and seed from Stone 3200 (Kaala, Oahu). At right, below, capsule and pistillate flower from Stone 2826 (Pupukea).

quite glabrous, often pale, greenish, or after dehiscence brown, dehiscent along the upper and lateral sutures; endocarp glabrous, pale, thin, late detaching; seeds often only one per carpel; testa crustaceous, shining black.

TYPE: L  veill   cites three specimens, all from Kalihi, Oahu, collected by Faurie: numbers 11, 217, and 217*bis*. No type is designated. A search was made for these specimens in the herbaria of the Bishop Museum, the British Museum, the Royal Botanic Gardens at Kew and at Edinburgh, the Museum d'Histoire Naturelle, Paris, Gothenburg Botanical Garden, U. S. National Museum, Gray Herbarium, Arnold Arboretum, Cornell University, etc., but without avail. Many of L  veill  s "types" are at Edinburgh or at the British Museum, but none of the cited specimens can be located. The original description is so short and noncommittal that alone it is meaningless: "Affinis praecedenti a quo tantum differt foliis longius 10-25 mm petiolatis, oppositis; petiolo nec rugoso, nec vulnerato, corymbis 2-5 floris, pedicellis bis bibracteolatis, apice incrassatis."

Rock (1914) reduced *Pelea oahuensis* to *P. molokaiensis* Hbd. β var. Hbd., on the basis of Faurie 217, which perhaps was at the Berlin Museum. The preceding species to which L  veill   refers in the above description is his own *Pelea waianaiensis*, which is more fully described. It is based on a single number (Faurie 215, isotype at Bishop), and is apparently a form of *Pelea peduncularis* L  vl. The reference, however, is helpful in interpreting the present species, as the two are similar in appearance.

In the absence of any type material, it seems necessary to designate a neotype, which would of course be replaced by original material should any turn up. The species, as interpreted here, is a very distinct and common one on Oahu, and is the Oahuan counterpart of the "moki-hana" or *Pelea anisata* Mann of Kauai; the same strong anisate odor is present in all parts, the flowers and fruits are very similar, and the specific differences are mainly in characters of the leaves and habit. There are a great many collections of this species, most of which have been determined as *Pelea Wawreana* Rock, which is, however, a very different species of

Sect. *Megacarpa*. The following collection may be selected as neotype:

NEOTYPE: Oahu: Waianae Mountains; Kunia trail, 26 March 1960, B. C. Stone & G. Pearsall 3282 (Bishop; duplicates to be distributed).

DISTRIBUTION: Endemic to Oahu. This is a very common species on both the Waianae and Koolau ranges. It may be identified in the field by its strong anise fragrance, very short essentially glabrous 3-5-flowered cymes with small greenish flowers, and small cuboid green or whitish-green capsules. In the Waianae Mountains it occurs in company with *Pelea peduncularis*, *P. kaalaensis*, *P. clusiaefolia* var. *crassiloba*, and *P. elliptica*.

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A Prior Name for the Hawaiian *Gouldia terminalis* (Rubiaceae)

ROBERT L. WILBUR¹

AMONG the most frequently encountered woody plants in the wetter, forested portions of the Hawaiian Islands are members of the extremely variable genus *Gouldia*. Fosberg (1937) presented the results of his detailed study of this baffling genus and concluded that the variability could be properly categorized in not less than three species composed of more than 90 varieties and forms. However, even this number of formally named taxa failed adequately to represent the variability, for hybridization was so rampant that at that time more than 50 hybrids were also recognized and characterized. It is therefore not surprising that *Gouldia* has acquired a reputation, among botanists working on Hawaiian plants, not unlike that of *Crataegus* and *Rubus* in the eastern United States. Like those genera, it is naturally felt that its taxonomy can now be handled only by a specialist. The present note, written far from Hawaii, is therefore merely concerned with the nomenclature of the most widespread and variable species of this endemic genus.²

Although members of the genus undoubtedly must have been collected by botanists on several expeditions prior to that of the "Rurik" led by Kotzebue, the first description of a species is apparently the detailed analysis provided by Chamisso and Schlechtendal (1829) of their "*Kaduae affinis*." Chamisso was the botanist on Kotzebue's voyage, and the original collection apparently was made on the slopes of the Koolau range of Oahu. Their account, as pointed out by Heller (1897), Fosberg (1937:4, 26) and Bul-

lock (1958), did not result in a published binomial at that time as was inferred by A. Gray (1860) and the *Index Kewensis* (1895). In spite of the unusually detailed analysis of the sixth species appearing in their newly described genus *Kadua*, Chamisso and Schlechtendal failed to provide a binomial for this plant; they merely indicated its close affinities to *Kadua*, from whose species it differed in its indehiscent fruit and toothed stipules.

The following year DeCandolle (1830) listed each of Chamisso and Schlechtendal's species and condensed the original detailed accounts of each into but a few lines. Their "6. *Kaduae affinis*" appeared in DeCandolle's *Prodromus* in the form quoted below:

6. K? AFFINIS (Cham. et Schlecht. 1. c. p. 164.) ramis tetragonis transversim rugosis, foliis elliptico-lanceolatis acutis basi obtusis breve petiolatis, stipulis membranaceis utrinque subdentatis deciduis, cyma thyrsioidea terminali, drupa subglobosa, limbo calycis oblitterato infra apicem coronata, indehiscente. [Woody tree or shrub] in insula O-Wahu. Flor. ignoti.

Fosberg (1936:4) dismissed DeCandolle's publication as a nomenclatural source in the statement quoted below:

DeCandolle, in 1830, a year after the publication of Chamisso and Schlechtendal's work, credited the latter with a '*Kadua- affinis* Cham. and Schlecht.,' appending a description which is an obvious condensation of the description published by Chamisso and Schlechtendal. DeCandolle's entire treatment of *Kadua* is based directly on the original treatment of the genus by Chamisso and Schlechtendal, with the same species arranged in the same order and with descriptions which are identical but somewhat condensed . . . It is obvious that '*Kadua affinis*' is the result of a misinterpretation of the intent of the original authors of the genus *Kadua*, as DeCandolle added nothing to the descriptions and no discussion. Therefore, it is evident that

¹ Department of Botany, Duke University, Durham, North Carolina. Grateful acknowledgment is made to the National Science Foundation for a grant of research funds to Duke University (NSF-Grant 18799) which made the present study possible.

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² Dr. F. R. Fosberg's thoughtful advice is here acknowledged with appreciation, but this does not imply that he is necessarily convinced of the change proposed in this paper.

DeCandolle did not have any intention of making a new species '*Kadua affinis*,' making it possible to judge it on the basis of Chamisso and Schlechtendal's original intent. The Cambridge Rules of 1930, Article 68, state that terms which are merely words, not intended as names, should be rejected; thus, fortunately, a means is provided for disposing of this meaningless name.

It would seem, however, that Fosberg's stated reasons are not sufficient justification for rejecting the name. Chamisso and Schlechtendal concluded in their final sentence concerning this species that "the whole internal structure of the fruit agrees therefore with *Kadua*."³ Although they did not publish a binomial, it certainly would appear that DeCandolle did. Chamisso and Schlechtendal expressed their doubts as to generic position in one fashion and did not provide the taxon with a name; DeCandolle was no more certain as to the generic position of the plants than the original authors, but he expressed his doubts as to generic position in a different manner and did provide a binomial. He was perfectly free to utilize the epithet *affinis*, which he did. The question mark following the abbreviation of the generic name merely indicated that he too was uncertain that the clearly described species actually was congeneric. Chamisso and Schlechtendal more than adequately described the species but failed to provide a binomial; DeCandolle provided a binomial even though admitting that the plant might eventually prove not to be a congener of the other five species. Although DeCandolle "added nothing to the description and no discussion," he did provide the binomial that the previous detailed description of the species lacked. Fosberg's conclusion that "it is evident that DeCandolle did not have any intention of making a new species *Kadua affinis*" seems unwarranted. DeCandolle provided a binomial, and there is certainly no evidence that his intentions were at variance with his accomplishment.

In the *Prodromus* DeCandolle did not customarily place any authority at all after names that he was proposing. Species and new combinations being there published by him were not followed by any authority or reference. Since

abbreviations for Chamisso and Schlechtendal, together with a reference to the place of publication, were all included parenthetically by DeCandolle after *K? affinis*, it might be argued that he was merely accepting Chamisso and Schlechtendal's treatment and had no intention of publishing a new name. This is impossible to prove one way or the other, but certainly Article 34, Note 2, of the *International Code of Botanical Nomenclature* (1961) was never meant to be applied in such a case, as is shown by the examples provided. Furthermore, DeCandolle employed the parenthetical citation to convey a variety of information in addition to his customary indication of author and place of publication. Other information characteristically conveyed parenthetically by DeCandolle concerned authors who had merely indicated a species as new on a herbarium specimen (e.g., *Eryngium Haenkei* Presl ex DC., Prodr. 4:94. 1830); or mention that a description of a new species has been provided in a letter by another (e.g., *Eryngium prostratum* Nutt. ex DC., Prodr. 4:92. 1830); or that a drawing had been seen in the herbarium (e.g., *Cornus disciflora* Moc. & Sessé ex DC., Prodr. 4:273. 1830). Certainly, since DeCandolle had not seen specimens of this Hawaiian species, it was in accord with his rather liberal usage of parenthetical citation to indicate the source of his information. It is certainly not necessary to conclude that DeCandolle was not aware that Chamisso and Schlechtendal actually had not published a binomial. The conclusion therefore seems to me inescapable that DeCandolle did originate a binomial that was the first published for this species.

A combination based upon DeCandolle's binomial, therefore, appears necessary for this extremely common Hawaiian species. Combinations for the multitudinous varieties and forms within this species, of which more than 85 were originally proposed by Fosberg, are not provided here; it would seem most undesirable for anyone not thoroughly familiar with these variants to make the numerous transfers apparently required. It seems probable that a restudy of the problem with the benefit of the numerous collections made during the past quarter of a century might very well reduce considerably the number of taxa worthy of recognition. However,

³ "Convenit ergo omnis interna fructus fabrica cum *Kadua*."

Skottsberg (1944*a, b*) has expressed the opinion that there are at least several times as many species as accepted by Fosberg, and he has provided binomials for a number of them by elevating certain of Fosberg's varieties and forms in addition to accepting some binomials of earlier authors. And, recently, the Degeners (1961) have also expressed a different view and, in so doing, provided 22 new combinations largely as a result of elevating Fosberg's taxa to the next highest rank. Therefore, it would not seem desirable to make wholesale transfers at the present time.

Gouldia affinis (DC.) comb. nov.

"*Kadua affinis*" Cham. & Schlecht., *Linnaea* 4: 164. 1829.

Kadua affinis [K? *affinis*] DC., *Prodr.* 4:431. 1830.

Petesia terminalis Hook. & Arn., *Bot. Beechy's Voy.* 85. 1832.

Petesia coriacea Hook. & Arn., *Bot. Beechy's Voy.* 85. 1832.

Gouldia sandwicensis A. Gray, *Proc. Am. Acad.* 4:310. 1860. *nom. illegit.* Art. 63 and 67.

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Population Dynamics in a Sublittoral Epifauna

WILLIS E. PEQUEGNAT¹

AT PRESENT we have little evidence that successional changes following predictable patterns occur among epifaunal communities living on natural rock-reefs in the shallow sublittoral of the open ocean. If this phenomenon does occur here, it can be detected by sustained observations at a single study site. In the period from 1957 to 1960 I conducted an intensive study of the epifaunas of two submarine hogbacks located at different depths off the coast of Corona del Mar, California. Some observations made during this period indicate that both gradual and disruptive changes do occur in these epifaunal communities. Attention is called in this paper to an abrupt change in population density of a predominant species that occurred on part of the shallower reef, and to the widespread biotal adjustments that ensued.

The epifauna of the deeper reef (9.5–18.5 m) remained quite stable throughout the study period (Fig. 1, Reef 500). Nevertheless, this is a dynamic stability with an appreciable flow of individuals through the community structure. For example, in the rock oyster, *Chama pellucida*, which is dominant on the upper part of this reef, natality and growth counterbalance mortality from all causes and such erosive factors as *Lithophaga* burrowings, resulting in a stable community as determined by consecutive samplings over a prolonged period. Some seasonal population fluctuations were observed, especially among sponges and ectoprocts, but I have not detected there any changes that can be construed as serial stages moving toward a climax differing from any extant community.

But this stability appears not to be characteristic of a significant part of the epifauna that

was present on the shallower reef (2–11.2 m) when the first observations were made (Fig. 1, Reef 200). Although the temporal changes in communities observed here cannot be presented as a typical ecological succession, they have had profound influences upon the composition of the epifauna of this rock-reef. My purpose in calling attention to these changes is to stimulate other investigators to follow the course of similar population shifts that may occur in regions under their purview. Additional data may make it possible to delineate the role of successional heterochrony in creating the complex epifauna present on submarine reefs at any given point in time.

The central species in the present study is the common mussel, *Mytilus edulis*. Beginning in late January, 1959, the *Mytilus* population on the inshore reef began a decline in density, which was not recognized as of singular importance at the time. However, before this decline leveled off it resulted in an almost complete disappearance of this species from the reef. The basic cause is unknown, although the early sharpness of decline suggests that disease may have been a contributing factor. Still, the decline did not occur on the deeper reef, some 300 m distant, although it must be pointed out that the maximum population densities here were only a hundredth of those on the shallower reef. In addition to the possibility of disease, it is known that an unusually large population of *Pisaster giganteus* was preying on the dense mussel population during preceding weeks. Although the decline extended through a year, the bulk of the *Mytilus* population disappeared in half this time. Unfortunately observations were not made during part of this period, nor has it been possible to follow developments after *Mytilus* was nearly wiped out. Nevertheless, sufficient data are available to provide a picture of the biotal shifts that accompanied the decline. The dis-

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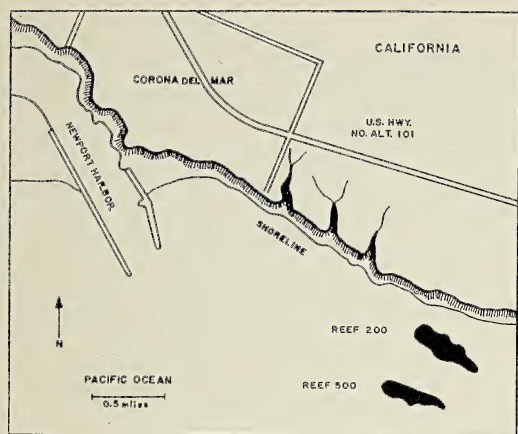


FIG. 1. Location of the two sublittoral rock-reefs under study, in relation to the city of Corona Del Mar and the entrance to Newport Harbor, Orange County, California.

appearance of certain predominant species apparently triggered increases and decreases in associated species. And these changes proved to be very extensive, involving some species that would not have been expected to react to changes in *Mytilus* populations.

STUDY SITE

The rock mass under study is composed of siltstone that has been subjected to complex folding. Gorsline (1962) advises that these promontories may properly be called submarine hogbacks. The dip of the strata ranges from a few degrees to 90° , but the larger part exhibits the latter dip. Because it is located approximately 200 m offshore, I shall refer to it hereinafter as Reef 200.

Situated about 2.5 km southeast of the entrance to Newport Harbor, Reef 200 (Fig. 1) rises from a sand bottom at a greatest depth of 11.2 m to a shallow point of 2 m at standard mean sea level. It has a minimum surface area of 1,200 m² distributed over a length of 58 m and an average width of 27 m (ranges from 8 to 44 m). Because its long axis parallels the shore, the hogback lies athwart the direction of surface wave propagation. This results in interference with wave transmission and a high degree of turbulence at shallow points. The magnitude of turbulence is inversely related to

depth; hence it falls off rapidly down the walls and is barely perceptible at the reef base on days of average swell.

Most of the *Mytilus* population was confined to the reef's flat top, between depths of 2 and 4 m. The same was true of such brown algae as *Eisenia arborea*, *Egrecia australis*, and *Laminaria farlowi*.

STUDY METHODS

Samples of the *Mytilus* populations of Reef 200 were obtained under water by using SCUBA. Quadrats were established by placing metal rings encompassing 0.1 m² against the biota and removing all components by hand. Where required, hammers, chisels, and forceps were also utilized. All specimens were placed in canvas bags, which were sealed prior to ascent and returned to the laboratory. Subsequently species were identified, and individuals of numerable species (noncolonial) were counted and measured.

Prior to the *Mytilus* decline, study sites were selected by dropping metal rings onto the reef from a moving boat. Samples were removed from the sites where the rings came to rest. During and after the decline, conscious attempts were made to remove samples within a few meters of predecline quadrats. This was possible since chisel marks were still evident on the rocks. The first samples were taken on October 29, 1958, and the last on February 22, 1960. The longest period without samples extended from February 15 to August 19, 1959, when the author was in Europe. For most purposes I have divided the dates of sampling into three periods of time: Predecline (October, 1958, to January 15, 1959), Decline (January 16 to October 15, 1959), Postdecline (October 16, 1959, to February, 1960). Although *Mytilus* had not disappeared completely from the reef at the end of the study, its average population per 0.1 m² quadrat was then only 0.5% of its original value. Twelve 0.1 m² quadrats were studied during the above periods.

Large species, such as *Pisaster giganteus*, *Strongylocentrotus purpuratus*, and *Parastichopus parvimensis*, were sampled with metal rings encompassing 1 m². Specimens of these species were not removed from the reef. Samples were

taken at random distances along transverse and longitudinal transects. Some 100 sq m quadrats were established during this study.

RESULTS

During the decline, the *Mytilus edulis* population at depths of 2 m dropped from an average of about 1,100 to less than 10 individuals per 0.1 m². Even more drastic reduction eventually occurred at greater depths (Table 1). And as *Mytilus* declined at specific sites, populations of the red alga *Corallina chilensis*, which are stated in terms of percentage of rock surface covered in Table 1, increased on the same sites, particularly above depths of 4 m. There was, however, a considerable lag between *Mytilus* depletion and the spread of *Corallina*. This lag permitted rapid population increases of a few invertebrates. But, as will be discussed later, some of these increases were cut back after the encroachment of *Corallina* got underway. In turn these population shifts triggered other reciprocal changes among less noticeable species, especially among platyhelminths, nemerteans, mollusks, annelids, and crustaceans (Table 2). Fortunately sufficient samples had been taken prior to, or early in, the *Mytilus* decline to establish a basis of comparison with subsequent unforeseen events. The samples of November, 1958 (Table 1), reveal (1) that most of the *Mytilus* population lived on horizontal surfaces at depths between 2 and 4 m, (2) that its density decreased sharply with increasing depth to the 7-m level, and (3) that

it was absent from this point downward. These relationships persisted unchanged as late as January 15, 1959. Soon thereafter, however, it was noted that *Mytilus* shells were beginning to accumulate in unusual numbers on the shoreward bottom of the reef. Unfortunately an impending trip to Europe precluded additional sampling for several months. But by August, 1959, the *Mytilus* population at the 2-m level (samples were taken only a few meters horizontally from the predecline quadrats) had dropped about 80%. And, as can be seen in Table 1, by February, 1960, considered here to be early post-decline, *Mytilus* had almost disappeared from the entire reef. Apparently at depths below 2 m the initial rate of decline was not as rapid, but complete disappearance eventually occurred. The later occurrence of small individuals at depths of 8 and 9 m is probably explained by dislodgment of small clumps from the reef-top. As seen in Table 1, *Corallina* increased markedly during this time, and came to form a uniform mat, some 6 cm thick, over much of the reef's upper surface. This trend continued until at the culmination of the study it covered 65% of the shallowest part of the reef with a mat some 9 cm thick.

Meanwhile significant changes occurred in molluscan populations. Whereas an average of 25 molluscan species per plot (among a total of some 35 species on all plots) occurred with *Mytilus* (at 2-m depths) prior to the decline, this average dropped to 11 by September, 1959

TABLE 1

CHANGES IN POPULATION DENSITIES, WITH DEPTH AND TIME, OF *Mytilus* AND *Corallina*
(Dashes indicate absence of data)

DEPTH (m)	<i>Mytilus edulis</i> : IND /0.1 M ² * BY DATE				<i>Corallina chilensis</i> : % COVER† BY DATE			
	11/58	9/59	10/59	2/60	11/58	9/59	10/59	2/60
2	1,086	176	95	5	5	25	50	65
4	180	90	0	0	5	10	15	35
6	95	50	0	0	—	5	5	10
7	7	20	0	0	5	—	—	0
8	0	0	7	0	—	5	5	—
9	0	7	0	0	0	0	0	—

* Individuals per quadrat.

† Per cent of quadrat surface covered by plant.

TABLE 2
DATA GATHERED FROM 0.1 M² QUADRATS AT 2-M LEVEL BEFORE, DURING, AND
AFTER MAJOR PART OF *Mytilus* DECLINE

PHYLA	NO. SPECIES IN PHYLA (Average)		
	Predecline	Decline	Postdecline
Porifera	2.5	1.5	2
Coelenterata	3	3	3
Platyhelminthes	2	3	4
Endoprocta	1	0.5	0
Ectoprocta	5	3.5	6
Sipunculoidea	1	1	1
Nemertea	1	1	3
Mollusca	25	11	25
Annelida	12	7	21
Arthropoda (Crustacea)	8	6.5	11
Echinodermata	4	2.5	5
Chordata (Ascidacea)	1	1	1
TOTAL ANIMAL SPECIES	66	48.5	82
Numerable Species	56	42	72
Motile Species	36	28	47
TOTAL ANIMAL INDIVIDUALS/0.1 M ²	1759	1754	841

(Table 2). Then, as the result of the encroachment of different molluscan species, it increased again to an average of 25 by February, 1960. Four types of population shifts were exhibited by molluscan species during this time: (1) the numbers of one species originally present increased, (2) several species declined but persisted, (3) others declined in numbers and eventually disappeared, and (4) previously absent species invaded the *Corallina* mat. *Chama pellucida* is the only species that increased and retained its population gain, although, as would be expected, the new individuals were very small. Twelve of the original 35 species suffered severe population drops, but were still present in February, 1960. Illustrative of these, in addition to *Mytilus edulis*, are *Hiatella arctica*, which dropped from an average of 135 to 10 individuals / 0.1 m², and *Pterorytis nuttalli*, which dropped from an average of 16 to 2 / 0.1 m². Twenty species of mollusks that were originally present disappeared completely. Among the more prominent of these are *Mytilus californianus*, *Modiolus capox*, *Tegula ligulata*, *Amphissa bicolor*, and *Glans carpenteri*. Among the 15 invading species are *Anomia peruviana*, *Chlamys hastatus*, *Flabellina iodinea*, *Doriopsilla fulva*,

and *Erato vitellina*. The following three species were unaffected by the other changes: *Crepipatella lingulata*, *Pholadidea penita*, and *P. ovoidea*.

Similar changes took place among the polychaetes. Whereas an average of 12 species occurred on *Mytilus* quadrats (2-m depth) prior to the decline, this dropped to 7 in October, 1959, and then rose sharply to 21 by February, 1960 (Table 2). The greatest increase was exhibited by *Nereis grubei*, which shot from an early average of 8 to 96 individuals / 0.1 m² by October, 1959. It persisted at or above 80 / 0.1 m² into February, 1960. The populations of *Anaitides mucosa* and *Platynereis* sp. more than doubled in this time. *Arabella iricolor* declined at first, but recovered its earlier population size by February, 1960. On the other hand, *Eunice rubra*, *Typosyllis pulchra*, *Polycirrus* sp., and *Polydora* sp. declined sharply and eventually disappeared. Eleven species of polychaetes, not previously present, invaded the *Corallina* mats. Among the more interesting of these are *Lumbrinereis zonata*, *Anaitides* sp., and *Nainereis dendritica*. None of the invading species came to be represented by many individuals.

Among the crustaceans, *Balanus tintinnabulum* displayed a marked population surge from

a predecline average of 30 individuals to 800 / 0.1 m² during the decline. This dropped back to an average of 350 living individuals per 0.1 m² by February, 1960. Curiously, *Balanus trigonus* populations remained unchanged throughout the period, as did those of *Pachycheles rudis*, *P. holosericus*, and *Crangon dentipes*. Four species of crustaceans disappeared during the *Mytilus* decline: *Paraxanthias taylori*, *Cirolana harfordi*, *Lophopanopeus leucomanus*, and *L. diegensis*, the latter of which had been represented only by young. These losses were more than offset by the appearance of six species, among which are *Pelia clausa* and *Pugettia dalli*.

Among the smaller echinoderms, *Ophiactis simplex* reacted quickly by nearly doubling its population at the 2-m level, going from 180 individuals to 340/0.1 m² by October, 1959. This dropped back to an average of 154/0.1 m² by February, 1960. The plankton-feeding holothuroid *Cucumaria lubrica* appeared on the 2-m level for the first time.

While working with the above data I was struck by the fact that throughout the entire period from November, 1958, to February, 1960, over 72% of the numerable individuals at the 2-m level were found in only four species (Table 3). We see, however, that the relative percentages that each contributed to the total shifted considerably during the decline.

Now let us turn to an analysis of shifts among the larger species existing on Reef 200. Not

only did populations of some of these decline significantly, but there were also shifts of population centers on the vertical axis. One might easily have predicted some, but not all, of these changes. Prior to the decline, 70% of the *Pisaster giganteus* population was found on the upper half of the reef in close association with *Mytilus* (Table 4). Subsequently this percentage dropped to 46. At the same time the *Pisaster* population on the entire reef dropped about 45%, presumably as a result of emigration to new sites. Most of the *Pisaster* emigrants must have come from the upper reef. Quite unexpectedly the sea urchin *Strongylocentrotus purpuratus* appears to have been markedly affected by the *Mytilus* loss. Its population dropped 34% and data in Table 4 point also to a downward movement on the reef. *Strongylocentrotus franciscanus*, on the other hand, suffered only a small loss of total population, and the center of population remained on the lower reef as before. The quadrat densities of the sea cucumber *Parastichopus parvimensis* dropped 30% during the *Mytilus* decline, but the center of population remained on the lower half of the reef.

DISCUSSION

Four kinds of population changes occurred during the *Mytilus* decline: (1) some species previously present with the mussel increased in numbers and held their gains; (2) some species

TABLE 3
PERCENTAGE OF TOTAL INDIVIDUALS OF NUMERABLE SPECIES ON EACH QUADRAT PROVIDED BY ONLY FOUR SPECIES

SPECIES*	PERCENTAGES OF TOTAL POPULATION BY DATE†				
	11/21/58	1/16/59	9/4/59	10/4/59	2/14/60
<i>Mytilus edulis</i>	61	62	10	5	0.2
<i>Balanus tintinnabulum</i>	2	2	40	46	42
<i>Nereis grubei</i>	0.2	0.7	4	5	10
<i>Ophiactis simplex</i>	11	10	20	22	20
PERCENTAGE OF POPULATION	74.2	74.7	74	78	72.2
NO. OF OTHER NUMERABLE SPECIES	53	50	50	26	68

* Note that these four species accounted for an average of 75% of the total animal population, but their relative contributions to the total changed markedly during the decline.

† Data obtained prior to (11/21/58) and during the *Mytilus* decline on the dates heading columns. All quadrats situated at depths of 2 m and within 3 m of the first.

TABLE 4

RELATIVE POPULATION DENSITIES OF LARGE, MOTILE SPECIES BEFORE AND DURING THE DECLINE OF *Mytilus* POPULATIONS

SPECIES	INDIVIDUALS/M ² *			
	Predecline		During Decline	
	depth (m)†		depth (m)†	
	2-7	7.1-11.2	2-7	7.1-11.2
<i>Pisaster giganteus</i>	3.3	1.7	1.2	1.5
<i>Strongylocentrotus purpuratus</i>	3.7	0.5	1.6	1.0
<i>Strongylocentrotus franciscanus</i>	0.5	5.8	1.1	4.8
<i>Parastichopus parvimensis</i>	0.1	0.6	0	0.5

* Average number of individuals per square meter.

† Reef is divided roughly into upper (2-7 m depth) and lower parts to show some redistribution of individuals of some species with depth.

appeared only after *Corallina* became predominant; (3) others maintained their populations at previous levels, though most underwent temporary fluctuations; and (4) still others decreased and, in some instances, disappeared. Most of the major population shifts occurred where *Mytilus* was previously dominant, but a few significant shifts were noted below the 4-m line. The degree of these effects may provide some measure of the closeness of relationship of individual species to the mussel (and to *Corallina*), both in positive and negative (inhibitory) ways. Our knowledge of these relationships will be increased significantly when careful studies are made of the feeding habits of the many species involved.

Some species increased in numbers simply because space became available and they had the reproductive capacity to spread out. *Balanus tintinnabulum* exemplifies this; its larvae were available to settle prior to the encroachment of *Corallina*. It is apparent, also, that *Corallina* is unable to invade an established *Mytilus* bed, but when the latter is gone the alga moves in after a few weeks' lag. Other species increased after this alga had become established, apparently because it provided a more suitable milieu. Quite possibly some species increased as a result of the withdrawal of predators not adapted to living in algal mats. The marked decrease in *Pisaster giganteus* resulted from an abrupt loss of food. The shift of remaining individuals to the lower

part of the reef is probably related to the presence there of *Chama pellucida*, an alternate food source. The anemone *Anthopleura* sp. dropped from an average of 40 individuals to 17/0.1 m² because of a reduction of substratum rather than of food. Prior to the decline most anemone individuals lived on mussel valves, with a few living in the rock niches. The number increased on the rock as the mussel declined, but the total available space was not sufficient to sustain the previous populations. The reduction of *Parastichopus parvimensis* may be accounted for by the greater production of detritus by *Mytilus* than *Corallina*, but this is purely conjectural. The different reactions of the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus* to the *Mytilus* decline indicate that broad generalizations are not appropriate. Whereas *S. purpuratus* suffered a severe decline, the other species was unaffected. It is perhaps significant that *S. purpuratus* existed primarily on the upper half of the reef, whereas *S. franciscanus* held forth on the lower half. The withdrawal of *S. purpuratus* may have resulted from the reduction of niches provided by the *Mytilus* beds and the fact that *Corallina* produced a very compact cover over the rocky surface.

Some interesting relationships between the numbers of species and individuals occurred during this disruptive change in community structure. These can be ascertained from the last four line items of Table 2. Note, for example,

that while the number of numerable (non-colonial) species per quadrat dropped about 25% during the decline, the total of individuals persisted unchanged for many months. But, as can be seen, by the beginning of the postdecline the total number of individuals in the numerable species fell markedly, in spite of the marked increase in numbers of species per quadrat. We find part of the explanation of this in the fact that when *Mytilus* was at its peak there was an average of 31 individuals per numerable species (aside from *Mytilus*) on each quadrat; that during the decline this jumped to 41, and then dropped to 12 in the early postdecline. These phenomena are based upon the following occurrences: (1) the rapid population increases of a few such species as *Nereis grubei*, *Balanus tintinnabulum*, and *Ophiactis simplex*; while (2) other species were leaving the sites; (3) formerly absent species, principally motile ones (Table 2), invaded the sites, resulting in an increase of 30% over the original number of species; (4) those species that underwent rapid population increases overshot the mark and dropped back; and (5) all of the invading species, at least during the period of this study, were represented by a small number of individuals. It is of interest that no single animal species equalled the former population density of *Mytilus*. *Balanus* came closest, but it is only a fraction the size of the mussel. This indicates that the animal contribution to the total biomass in the Hyperbenthal Zone (Pequegnat, 1961) was markedly reduced; the emigrations of the echinoderms mentioned above also account for a considerable loss. Reciprocally, the plant component must have risen through the *Corallina* increase.

For several reasons the appearance of the *Corallina* mat and associated species appears to

comprise an unstable complex. Judging from the population changes discussed above and from observations made elsewhere in the subtidal and intertidal, one gains the impression that extremely dense growths of *Corallina* are associated with disturbed conditions. Though one might expect this predominance of the corallines to be temporary, Dawson (1959) points to the distinct possibility that the corallines encroach upon and later dominate areas subject to pollution from human wastes. Hence interest is heightened in obtaining additional samples in the future.

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Preliminary Report on the Marquesan Sardine, *Harengula vittata*, in Hawaii

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THE MARQUESAN SARDINE, *Harengula vittata*, was introduced to Hawaiian waters in eight plantings from 1955 through 1959 by the Bureau of Commercial Fisheries in an attempt to establish this species as a supplementary bait fish for skipjack fishing. The details of the first seven introductions have been reported by Murphy (1960) and the eighth by Brock (1960). The eighth introduction comprised an estimated 4,000 sardines ranging from 7.0 to 9.4 cm in standard length² and averaging 8.2 cm. This brought the estimated total number of sardines introduced to Hawaii to 144,000. All of the releases have been made around the island of Oahu (Fig. 1).

SOURCES OF INFORMATION

The introduction of the sardines was publicized by means of posters and letters. Commercial and sport fishermen and game wardens were asked to cooperate in supplying information on sightings and captures. Jars of formalin and labels for recording data concerning captures were supplied to the game wardens and the skipjack fishermen, whose bait nets were considered a likely source of specimens. From 1956 through 1960, 54 samples comprising 336 fish were turned in, the majority of them by skipjack fishermen.

DISTRIBUTION

Recaptures of Marquesan sardines have been reported from six of the eight major islands in

Hawaii (Fig. 2). The lack of reports from Lanai and Niihau may be due to the fact that skipjack fishermen rarely fish for bait in the waters around those islands.

Table 1 lists all the sardine recoveries from the Hawaiian Islands. The first recapture was made in Keehi Lagoon, Honolulu, in 1956. Subsequent recoveries were from Barber's Point and Kaneohe Bay, Oahu, in 1957. In 1958 sardines were taken at the islands of Kauai and Maui, where no releases had been made, and also in Honolulu Harbor and Pearl Harbor, Oahu, for the first time. In 1959 the sardine was reported from the islands of Hawaii and Kahoolawe, and for the first time from Haleiwa, Oahu. The first specimens from Molokai and from Nawiliwili and Hanamaulu bays, Kauai, came in 1960. Sardines have been taken from both the leeward and windward shores of Oahu and Kauai but only from the leeward shores of Hawaii, Maui, Kahoolawe, and Molokai (Fig. 2).

Neither our knowledge of the life history of this species nor our observations of it in Hawaiian waters are adequate to tell us whether the extension of its distribution from Oahu to the other islands has come about through migration of the adults across the channels or through the drifting of eggs or larvae with the currents.

The habitat occupied by the sardine seems to coincide with that of the nehu, *Stolephorus purpureus*, the most commonly used tuna bait fish in Hawaii. This distribution pattern may be only a sampling artifact, since most of the fishing with gear likely to take sardines is done by skipjack fishermen fishing for nehu. However, because of the chronic shortage of tuna bait in Hawaii, the fishermen are alert for reports of bait supplies even in areas outside the usual nehu fishing grounds. If sardines were present in conspicuous abundance in any accessible area, it appears highly probable that the fishermen

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² All of the length measurements appearing in this report are expressed in standard length, which is the distance from the tip of the snout to the end of the hypural.

TABLE 1
RECORDS OF MARQUESAN SARDINES COLLECTED IN HAWAII

LOCALITY	DATE OF CAPTURE	METHOD OF CAPTURE	NUMBER CAUGHT	NUMBER PRESERVED	STANDARD LENGTH (cm)	
					Range	Mean
Oahu I. Keehi Lagoon	9/27/56	night net ¹		1	9.97-	9.97
	3/27/57	night net ¹		1	8.50-	8.50
	10/4/59	night net ¹	est. 500	17	3.59-5.60	4.40
	11/3/59	night net ¹		7	5.25-5.68	5.46
	11/5/59	night net ¹		27	4.08-6.07	4.88
	11/25/59	night net ¹		16	4.03-6.46	5.51
	12/1/59	(?)		2	3.05-3.51	3.28
	7/20/60	day seine	est. 3	1	2.92-	2.92
	9/14/60	day seine		3	3.39-4.72	4.27
	3/26/57	day seine	est. 7	1	8.75-	8.75
	4/8/57	night net		4	8.07-8.75	8.46
	6/4/57	night net		1	9.50-	9.50
	6/30/58	(?)		1	9.75-	9.75
	9/23/58	day seine		1	5.60-	5.60
	11/3/58	day seine		1	3.46-	3.46
	11/27/58	day seine	est. 12	6	3.53-4.30	3.96
	7/20/59	day seine	16	8	4.30-13.21	7.66
	9/4/59	day seine		2	4.90-8.56	6.73
	9/6/59	day seine		2	3.04-3.22	3.13
Kaneohe Bay	9/11/59	day seine		1	8.30-	8.30
	9/14/59	day seine		2	8.21-8.67	8.44
	10/2/59	day seine		1	5.40-	5.40
	2/26/60	day seine		1	12.01-	12.01
	6/9/60	day seine		2	3.34-3.68	3.51
	9/9/57	gill net		6	11.20-13.50	12.55
	2/28/58	night net		4	7.71-9.40	8.72
	6/27/58	night net		1	9.54-	9.55
	4/29/58	day seine		3	10.05-10.71	10.45
	9/2/59	day seine		11	4.46-6.10	5.27
Barbers Point Honolulu Harbor	6/22/60	day seine	est. 20	5	3.98-5.14	4.54
	7/22/60	day seine		2	4.71-8.64	6.67
Pearl Harbor Haleiwa	7/5/58	(?)	1	10	not exam.	not exam.
	10/7/58	day seine		29	3.49-5.32	4.67
	11/3/58	day seine		4	6.32-7.00	6.59
	5/19/59	day seine	est. 6	1	9.12-	9.12
	5/28/59	day seine		7	9.10-10.91	9.91
	5/29/59	day seine		2	9.29-10.83	10.06
	6/2/59	day seine		1	8.56-	8.56
	8/13/59	day seine		3	5.62-6.00	5.87
Maalaea Bay						

¹ The net used in Hawaii for taking tuna bait at night is a rectangular lift net pulled under the fish which are attracted to an underwater light suspended alongside the fishing boat.

² A "bucket" of bait in the Hawaiian skipjack fishery is estimated to represent about 7 lb of fish.

TABLE 1—*Continued*

LOCALITY	DATE OF CAPTURE	METHOD OF CAPTURE	NUMBER CAUGHT	NUMBER PRESERVED	STANDARD LENGTH (cm)	
					Range	Mean
Kauai I. Port Allen	9/10/58	night net		6	6.17–6.69	6.41
	10/2/58	night net		6	3.90–7.90	6.60
	5/24/60	day seine	est. 100	3	3.80–7.34	5.05
	7/5/60	day seine	est. 500	10	4.00–6.87	5.45
	7/9/60	day seine	est. 100	58	5.85–8.75	7.24
	7/23/60	day seine	est. 20	7	4.67–5.99	5.54
	9/25/58	(?)		6	6.90–7.90	7.50
	1/2/59	pole-and-line		2	9.80–11.48	10.64
Hanalei Bay Waimea Bay	10/14/59	pole-and-line		1	14.62–	14.62
	7/23/60	day seine	est. 40	2	11.34–13.30	12.32
						
Nawiliwili Harbor Hanamaulu Bay	6/2/60	night net		8	10.57–12.47	11.75
	9/6/60	gill net		1	12.21–	12.21
Hawaii I. Kawaihae Bay	3/14/59	day seine	est. 3 bkts. ²	12	7.56–10.05	8.73
Kahoolawe I. SW Point	6/17/59	day seine	est. ½ bkt.	11	9.76–12.08	10.83
Molokai I. Laau Point	9/3/60	day seine		5	5.61–6.70	5.80

would find them. The main nehu baiting areas are in the relatively protected waters of bays, harbors, and canals where the water is brackish and turbid owing to the influx of streams and ground water. The Kihei area on the island of Maui and Waimea on Kauai are exceptions, the baiting grounds being exposed to the open ocean and moderate surf action. Baiting, in general, is done close to shore in shallow water, although night-lighting for bait may be done in deeper waters of channels and harbors. Since it appears that the sardine has established itself in the nehu grounds, it is important, from the standpoint of the tuna fishery, to keep a close watch on the population trend of the species in Hawaii and the effect that it may have on the bait supply in the future.

ABUNDANCE

Our only source of information on the abundance of sardines in Hawaiian waters has been the reports of observations by commercial and sport fishermen. The numbers of specimens turned in by fishermen are not a good index of abundance, because often they are only a small and arbitrarily selected fraction of the catch. There have also been times when sardines were seen but not caught.

The first observation of a large school of sardines, 20 to 30 buckets,³ was made in Waimea, Kauai, late in the summer of 1958 by skip-

³ A "bucket," the unit commonly used by skipjack fishermen for measuring bait, contains an average of 7 lb of fish.

TABLE 2
PERCENTAGE FREQUENCY OF OCCURRENCE OF VARIOUS ORGANISMS IN THE
STOMACHS OF 93 SARDINES

LOCALITY (No. of fish examined)	COPEPODA	GASTROPOD LARVAE	SHRIMP ADULTS & LARVAE	CRAB LARVAE	FISH LARVAE	AMPHIPHODA	POLYCHAETA	BARNACLE CYPRIS	STOMATOPOD LARVAE	HETEROPODA (<i>Atlantia</i> sp.)	LUCIFER	PELECYPOD LARVAE	CHAETOGNATHA	OSTRACODA	ISOPODA	INSECT LARVAE	MYSIDACEA	PTEROPODA	CLADOCERA
Oahu I.	67	...	...	33	...	...	33	...	...	...	...	...	...	...	...	...	...	...	...
Honolulu Harbor (3)	100	50	8	...	...	25	50	...	...	...	...	17	...	...	8	8	8	...	...
Haleiwa (12)	94	31	38	31	12	12	25	31	12	...	...	6	...	...	6	...	...	...	6
Kaneohe Bay (16)	60	20	60	80	...	20	...	...	...	...	...	...	...	...	20	...	20	...	...
Barbers Point (5)	100	...	17	33	8	17	17	...	8	...	17	...	8	17	...	...	...	...	...
Keehi Lagoon (12)	73	33	20	13	27	7	...	7	20	...	...	...	13	7	...	7	...	...	...
Maui I.	12	...	...	...	100	...	12	...	...	...	...	...	...	...	...	...	...	...	...
Kihei (15)	100	...	20	40	...	80	...	20	40	...	100	...	...	...	...	20	...	...	...
Hawaii I.	100	...	20	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Kawaihae Bay (8)	100	...	20	40	...	10	...	10	...	80	...	...	20	...	...	...	...	20	...
Molokai I.	100	40	80	20	...	33	...	...	...	...	...	33	20	17	...	...	...	...	...
Lau Point (5)	100	40	80	20	...	...	...	10	...	...	...	...	...	...	...	...	...	...	...
Kahoolawe I.	83	...	...	67	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
SW Point (10)	...	...	...	...	100	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Kauai I.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Port Allen (6)	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Waimea Bay (1)	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
All areas combined	82	28	26	26	17	17	15	9	9	9	8	6	5	4	4	3	2	2	1

The food habits of the larger and smaller sardines appeared to be essentially similar, but fish larvae were found only in sardines 8.0 cm long or larger, and there seemed to be a size-associated difference in the composition of the copepod component of the diet. The smaller fish fed more commonly on small cyclopoid copepods, such as *Corycaeus* sp. and *Oncaea* sp., while the larger sardines had more often been

feeding on larger calanoids, such as *Candacia* sp., *Labidocera* sp., and *Pleuromamma* sp. The samples were inadequate to carry on a detailed study of food habits among the different areas.

As indicated in Table 2, 17% of the stomachs with food had fish larvae in them. Of 34 fish larvae found, 24 (71%) were identified as nehu. The largest number of larval nehu found in a stomach was 6, in a 10.8-cm specimen from Kihei, Maui. The largest nehu found measured 3.3 cm, in a 9.4-cm sardine, also from Kihei, Maui.

The food habits of *H. vittata* in its native environment were extensively studied by Nakamura and Wilson (MS). They also found copepods to be the most frequently occurring organism (79.1%), followed by pelecypods, gastropods, barnacle cypris, pteropods, amphipods, and megalops. Fish larvae occurred in only 1.6% of the stomachs. The only distinct difference between the feeding habits of the species in Hawaii and in the Marquesas seems to be the low percentage of occurrence of fish larvae in the Marquesan fish.

The food habits of the sardine in Hawaii are similar to those of the nehu, both species feeding largely on the crustacean elements in the plankton. Hiatt (1951) found that nehu feed primarily on copepods, barnacle larvae, mysis larvae of shrimps, ghost shrimp (*Lucifer* sp.), crab larvae, and palaemonid shrimps.

SPAWNING

The size of the first sardines taken at Maui and Kauai in 1958 was such that, as pointed out by Murphy (1960), it seemed more likely that they were the products of spawning in Hawaiian waters rather than members of the original transplanted stock. A collection of 29 sardines taken at Kihei, Maui, in October, 1958, contained 7 measuring less than 4.3 cm, which was the length of the smallest sardine measured in the release of May, 1958. Subsequently, sardines smaller than 4.3 cm were taken in Keehi Lagoon and Kaneohe Bay in July, September, October, November, and December, 1959 (Fig. 3). In 1960, small sardines were caught at Keehi Lagoon, Kaneohe Bay, and Haleiwa on Oahu, and at Port Allen, Kauai, in May, June, July, and September.

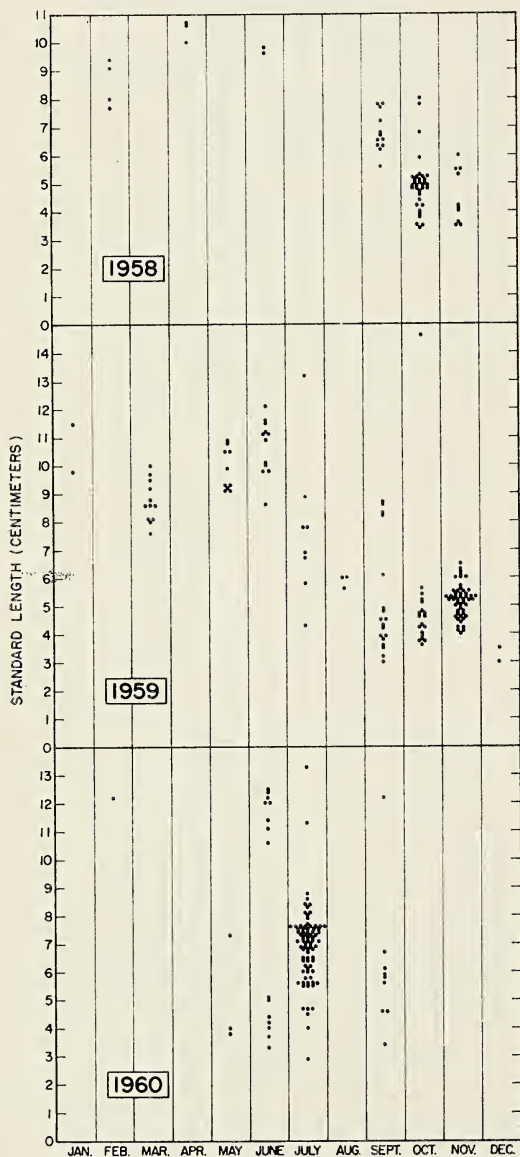


FIG. 3. Size frequencies of sardines collected in Hawaii in 1958, 1959, and 1960.

Nakamura and Wilson (MS) have reported that in the Marquesas 8.4 cm, plus or minus 1.7 cm, is the mean length of females at sexual maturity. They considered that year-round occurrence of ovarian eggs of 0.6 mm or larger diameter indicated that sardines spawn throughout the year in Marquesan waters. Although our Hawaiian samples were inadequate for determination of the spawning season of the introduced fish, the occurrence of ova 0.43 to 0.74 mm in diameter in sardines taken in May, June, July, September, and October and the appearance of small sardines from May through December lead us to believe that the species also has a prolonged spawning period in Hawaii.

SUMMARY

Eight releases of the Marquesan sardine, *Harengula vittata*, have been made around the island of Oahu in the hope that it would become established and sufficiently abundant to increase the tuna bait fish supply. An estimated 144,000 individuals were released from 1955 through 1959. Recoveries by skipjack fishermen have been made from all of the major islands except two. The habitat occupied by the sardine seems to coincide with that of the most important native bait fish, the nehu (*Stolephorus pur-*

pureus). The occurrence of young sardines since 1958 indicates that they have spawned successfully, but the species is not yet making any significant contribution as a bait fish. The sardines feed primarily on copepods, and also eat gastropod larvae, larval and adult shrimps, crab larvae, fish larvae, amphipods, and polychaetes. This diet is similar to that of the nehu.

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Hawaiian Records of Folliculinids (Protozoa) from Submerged Wood¹

DONALD C. MATTHEWS²

ABSTRACT: To folliculinids in Hawaii, taken from naturally submerged objects (*Halofolliculina annulata*, *Ascobius simplex*, *Metafolliculina andrewsi*) and from submerged glass-plate panels (*Metafolliculina nordgardi*, *Parafolliculina violaceae*), are added those from Douglas fir panels riddled by subsistent teredines and *Limnoria*: *Eufolliculina lignicola*, *Mirofolliculina limnoriae*, and *Lagotia viridis*. Variations in loricae and moniliform nuclear components are illustrated and discussed.

THUS FAR five species of folliculinids embracing four genera have been recorded for Hawaii (Matthews, 1962). Of these, *Halofolliculina annulata*, *Lagotia simplex*, and *Metafolliculina andrewsi* were taken from submerged naturally-occurring objects, whereas *Metafolliculina nordgardi* and *Parafolliculina violaceae* were taken from submerged glass-plate panels.

Douglas fir (*Pseudotsuga taxifolia*?) frames supporting these panels (Matthews, 1962, fig. 1), subsequently honeycombed by subsistent teredines and *Limnoria*, were broken apart; the tortuous burrows and their sequestered organisms revealed the folliculinids recorded here.

Folliculina lignicola, Fauré-Fremiet 1936, La famille des Folliculinidae. Mém. Mus. d'Hist. Nat. de Belg. (Ser. 2), 3:1129-1175.

Eufolliculina lignicola, Hadzi 1951.

This slender folliculinid (reassigned by Hadzi [1951] to *Eufolliculina lignicola* [Fauré-Fremiet]) was abundant in tracheids opened by burrowing gribbles. In riddled wood frames examined November 21, 1961 (corroborated January 11, 1962) *E. lignicola* was the most abundant, although not the most sequestered, folliculinid. In fact, just outside the burrows,

attached especially to calcareous tubes of serpulid worms (*Spirobis* sp. and *Mercierella* sp.) were numerous folliculinids whose sacs, necks, and moniliform nuclei fell well within those limits prescribed for *E. lignicola*. Thus, as suggested by Mohr (1959: 86) *E. lignicola* is not restricted to tracheids. Mention should be made, however, that although they were abundant on calcareous tubes of serpulids, none was attached to calcareous walls of abandoned teredo burrows, shells, or pallets, although these apparently afforded similar attachment potentials.

As frequently observed in other folliculinids, sac length, width, and height often varied with site conditions. In young colonies, composed of few folliculinids, ample space resulted in normal sac formation; whereas in old colonies, composed of many folliculinids, limited space resulted in "abnormal" sac formation. Thus, sacs lying contiguously were usually longer, whereas those laid one on another were usually shorter, etc. Despite their occurrence on serpulid shells, certain restrictive sites seemed preferred. A common restrictive site is illustrated in Figure 1. Although the neck (*c*) was free and always extended at an angle from the opened portion of a tracheid (*b*), the sac (*f*) usually was confined, at least in part, in the unopened portion (*g*). This condition, which resulted in a long narrow sac (up to 166 μ), affected in no way either the length of the neck (*c*) or the number of its spiral whorls (*d*). Thus, regardless of the

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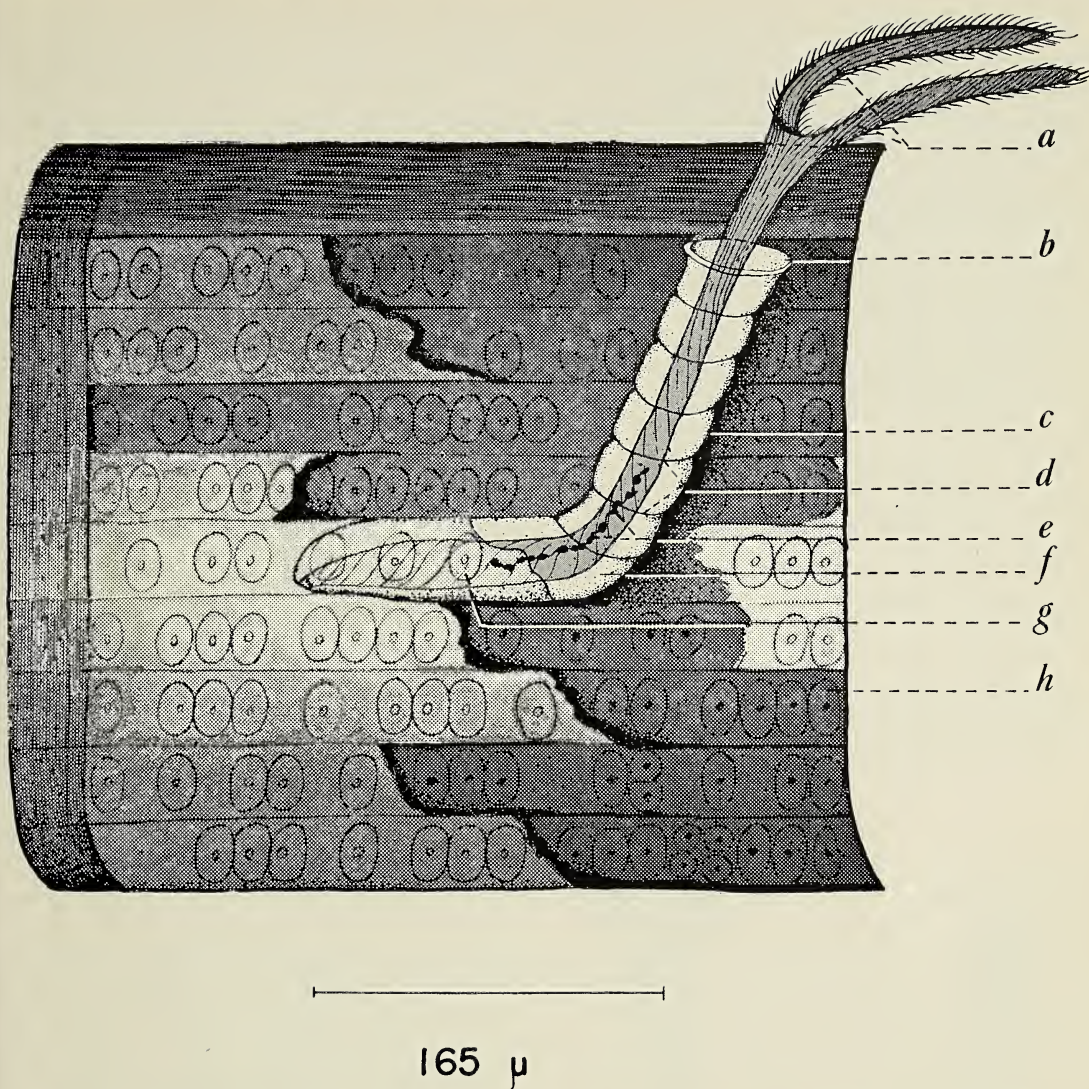


FIG. 1. *Eufolliculina lignicola*, as viewed from the right side showing: *a*, extended peristomal lobes; *b*, distal opening of neck; *c*, neck; *d*, spiral whorls; *e*, nuclear components; *f*, sac; *g*, unopened portion of tracheid; *h*, opened portion of tracheid.

site chosen, neck lengths varied only between 132μ and 167μ with the mean at approximately 159μ . Spiral whorls (*d*) usually numbered six, although occasionally five and seven were observed. The diameter of the neck (49μ) was approximately that of the unrestricted sac.

In reflected light the color of the extended body resembled that of *Parafolliculina violaceae* (Matthews, 1962), except that perhaps in *E. lignicola* the wine color was somewhat more

intense. However, in transmitted light the body and lorica appeared bottle-green, a characteristic of most folliculinids. As previously reported (Matthews, 1962), both size and number of nuclear components varied in accordance with body contraction resulting from fixation. Thus, in contracted bodies, nuclear components were large (5μ) and often numbered as few as 6, whereas in more relaxed bodies, nuclear components (Fig. 1*e*) were small (3μ) and often

numbered as many as 12. The peristomal lobes (*a*) were long (approximately 116μ) and in feeding specimens, were carried high above the distal opening of the neck (*b*). No swimmers were observed.

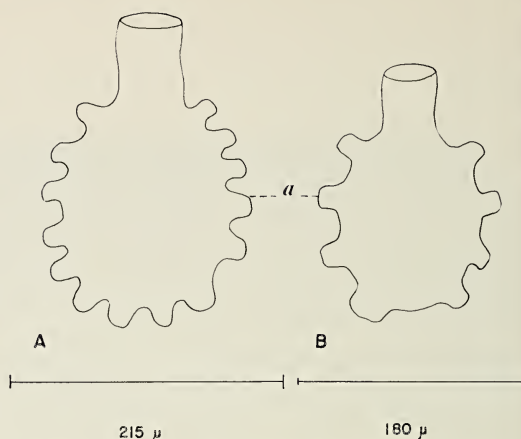
Mirofolliculina limnoriae (Giard 1883) Dons 1927 (*vid.* Fig. 2*A* and *B*)

Freya limnoriae Giard, Bull. Scientific, t.XV: 264–265, 1883.

Folliculina limnoriae (Giard) Fragments biologiques XIII. Sur les genres *Folliculina* et *Pebrilla*. Bull. Sci. Nord. 3:310–317, 1888.

Since Giard's publication of *Folliculina limnoriae*, this bizarre folliculinid has been characterized both by its habitat (dorsal surface of *Limnoria* pleotelson or adjacent segments) and by the lateral outpocketings of its lorica (Figs. 2*A*, *B*; 3*A*, *B*; 5*A*, *B*; 6).

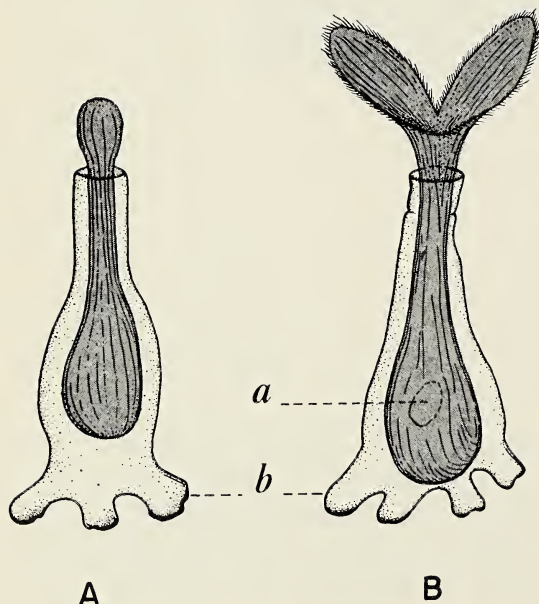
Although both Mohr (1959: 86), working on *Limnoria lignorum* of the Pacific coast of North America (Friday Harbor), and Giard (1888:314), working on *Limnoria* (sp.) of the



FIGS. 3*A*, *B*. *Mirofolliculina limnoriae*, showing: *a*, empty loricae with lateral pouches.

Atlantic coast of France (Wimereux), consider *M. limnoriae* an abundant species, rarely was it observed on *L. (Paralimnoria) andrewsi* (Coleman) of Hawaii (Menzies, 1959:10). In fact, not until November 29, 1961, after hundreds of gribbles had been examined, were even the empty loricae (Fig. 3*A*, *B*) observed. This paucity may in part be due to the fact that *M. limnoriae* temporarily had lost its habitat to another, as yet undetermined, organism; for, almost covering the dorsal surface of the pleotelson of every third or fourth gribble examined, was a large brown hemispherical cyst (Fig. 4*a*) which, when opened, liberated two minute unpigmented dorsoventrally flattened worms. This impression is further supported by the fact that during January, 1962, while the numbers of these cysts decreased, the numbers of *M. limnoriae* increased. However, even in old established gribble colonies (such as those from the riddled hull of the "Seth Parker" at Coconut Island) only one *M. limnoriae* was taken for every 21 *L. (P.) andrewsi* examined.

Of 25 *M. limnoriae* taken at random, the length of the sac varied from 133μ to 216μ , with the mean at approximately 149μ . The sac at its greatest width varied from 83μ to 132μ , with the mean at approximately 116μ . The neck, which was completely devoid of spiral thickenings or proximal lip, varied in length from 49μ to 66μ , with the mean at approximately 59μ .



FIGS. 2*A*, *B*. Tracings of Giard's plates of *Folliculina limnoria* taken at Wimereux showing: *a*, spherical nucleus; *b*, extent and region of pouches. Magnification not given.

The diameter of the neck was almost uniformly 50μ , except for those of certain empty loricae whose necks were ellipsoidal; in such instances the greater diameter (at right angle to the longitudinal axis) was roughly 58μ and the lesser diameter 25μ .

The greatest variation was observed in the number, arrangement, and size of the lateral pouches (Figs. 2A, B; 3A, B; 5A, B; 6). Although smaller loricae usually exhibited fewer pouches, this was not always the case. For example, a lorica (Fig. 5A) with but 6 pouches (the smallest number observed) was larger than a lorica (Fig. 5B) with 16 pouches. (Nineteen was the largest number observed.)

Although each lorica was somewhat swollen at its base, the pouches did not necessarily extend, as did those shown by Giard (Fig. 2A, B), in finger-like protrusions from the swollen base, nor were they bilaterally arranged. Arrangement of pouches varied from as few as 2 pouches on one side and 4 on the other (Fig. 5A) to as many as 9 on one side and 10 on the other (Fig. 6). Figure 5B is interesting for not only does it show a bilaterally symmetrical arrangement of the 16 pouches, but the anterior 2 (*a*) are clearly seen through the neck when viewed dorsally; hence similar outpocketings (as

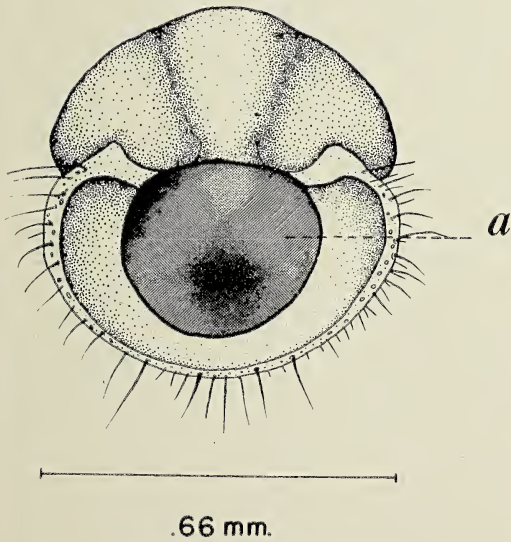
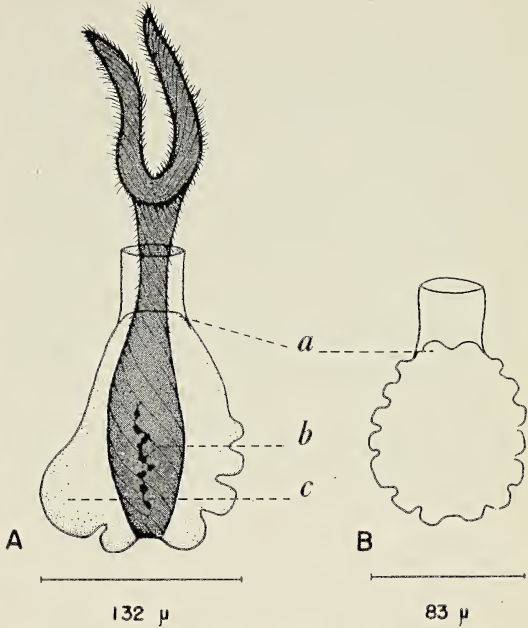


FIG. 4. Pleotelson of *L. (Paralimnoria) andrewsi*, showing: *a*, large hemispherical cyst on dorsal surface.



FIGS. 5A, B. *Mirofolliculina limnoriae* as viewed from the dorsal surface, showing: *a*, pouches visible through neck; *b*, lobes of moniliform nucleus; *c*, large, lateral pouch.

in Fig. 6*a*) may have been mistaken for the so-called valves mentioned by earlier investigators.

Even more variable was the size of the lateral pouches. These ranged from only a few microns (Fig. 6*b*) to half the width of lorica (Fig. 5A, *c*). And, although large pouches were usually located posteriorly near the base of the lorica, occasionally they were located anteriorly near the neck. Because to my knowledge the process of lorica formation in this species has not been observed, neither pouches nor their variation in number, arrangement, and size can at present be explained.

Unfortunately, too many observers have been concerned with the unique lorica and too few with the living organism. Even actual descriptions are meager. Giard (1888:315), who attributed to this species a non-moniliform nucleus (Fig. 2B, *a*) merely states "... [it] is a little smaller than the preceeding species [*Folliculina abyssorum* Giard], of a darker greenish blue with the striation of the integument less apparent. ...". Kahl (1932) is concerned that

folliculinids of quite varied nuclear components have been assigned to *M. limnoriae*. This is understandable. Since many different species of *Limnoria* have evolved in various regions of the world (Menzies, 1959) one would not expect the folliculinids, with which they are so intimately associated, to have remained constant. In *M. limnoriae*, as was previously pointed out for *E. lignicola*, nuclear components varied with the degree of body contraction following fixation. With peristomal lobes well contracted into the lorica, the nucleus appeared as little more than a dark spherical mass near the point of the body attachment. However, with peristomal lobes relaxed and carried high above the distal opening of the neck, the nucleus appeared as a string of beads whose size and numbers of components

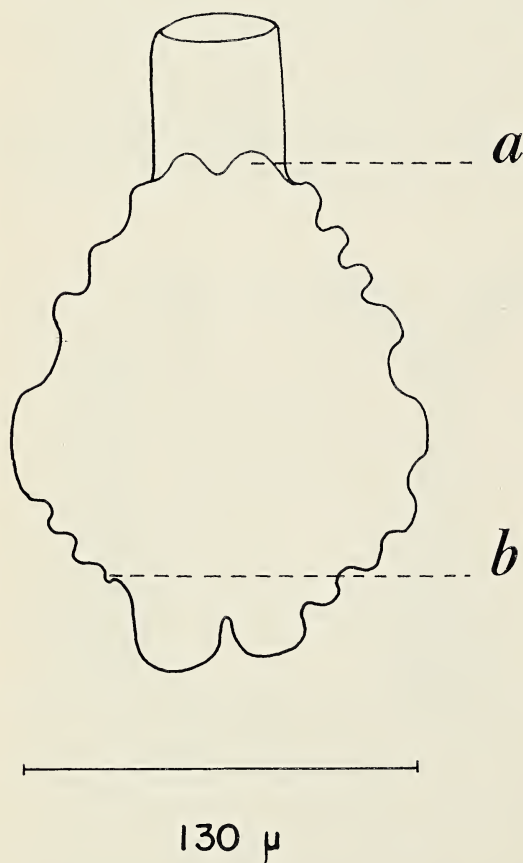


FIG. 6. *Mirofolliculina limnoriae* as viewed from the dorsal surface, showing: *a*, pouch viewed through neck; *b*, an extremely small pouch.

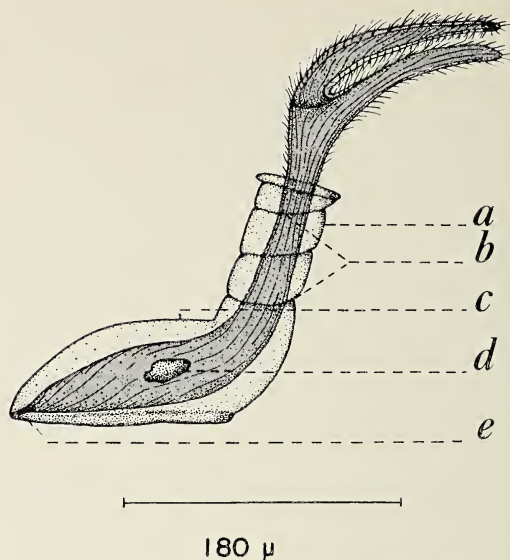


FIG. 7. *Lagotia viridis*, as viewed from the right side, showing: *a*, neck; *b*, three spiral whorls; *c*, non-flattened sac; *d*, spherical nucleus; *e*, non-spatulate foot.

varied. The largest number of nuclear components (Fig. 5A, *a*) observed was nine (and this was not in a completely relaxed specimen). The question of whether variations in nuclear components and/or variations in number, arrangement, and size of lateral pouches have specific value must await further and more extensive investigations. However, as mentioned by Mohr (1959) some correlation seems to obtain between the latitude in which *M. limnoriae* is found and the degree to which its lorica is branched (compare Giard's figure of *M. limnoriae* from France [Fig. 2A, B] with my figure of *M. limnoriae* from Hawaii [Fig. 6]).

Lagotia viridis, T. S. Wright 1858. Description of New Protozoa. Edinb. New Phil. Journ. New Series, 7:276-281.

While not directly attached either on or in riddled wood panels, *L. viridis* was abundant on and in the empty osseous valves of the prionodesmacean mollusk *Ostrea virginica*, which was present on all panels observed. Although, in an earlier publication (Matthews, 1953) *Lagotia simplex* (Dons, 1917) (reassigned by Hadzi, 1951, to *Ascobius simplex*) was also credited with occupying this habitat, there is no

good reason to confuse these related but quite distinct species. Although both species are devoid of vestibule and closing apparatus (valves) and possess spherical nuclei, Hadzi is justified in his reassignment of *L. simplex* to *Ascobius simplex* on the basis of its flattened lorica and spatulate foot; whereas in *Lagotia viridis*, the lorica (Fig. 7c) is not flattened nor is the foot spatulate (e). For representatives of *L. viridis* in Hawaii an even more obvious difference is at once apparent. Whereas in *Ascobius simplex* the neck is exceedingly short (Matthews, 1952: 344), in *Lagotia viridis* (Fig. 7) the neck (a) extends from the sac and is strengthened by two or three spiral whorls (b). Moreover, while *A. simplex* is comparatively small, *L. viridis* is comparatively large, often possessing sac lengths of over 180 μ and neck lengths of over 100 μ .

Thus, to date, folliculinids embracing eight species and seven genera are known from Hawaii. Accepting Hadzi's reassignments, these now stand as: *Halofolliculina annulata* (which I have not yet taken), *Ascobius simplex*, *Metafolliculina andrewsi*, *Metafolliculina nordgardi* (which may prove to be a new species), *Parafolliculina violaceae*, *Eufolliculina lignicola*, *Mirofolliculina limnoriae*, and *Lagotia viridis*.

It is interesting to note that, whereas *Folliculinopsis gunneri* Dons 1927, reassigned by Hadzi (1951) to *Pachyfolliculina gunneri*, is present on the ventral surface of *Limnoria lignorum* from the Pacific coast of North America (Mohr, 1959:86), not one specimen has been observed on the hundreds of *L. (P.) andrewsi* which I have examined.

There is every good reason to believe that new records of folliculinids from Hawaii will continue to appear. Re-examination of rather an extensive pagurid collection made over the past 10 years discloses many folliculinids which previously had been overlooked. Although these possess undamaged loricae, their still pigmented but highly contracted bodies are not suitable for specific determinations.

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Investigations of Rhinoceros Beetles in West Africa¹

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IN APRIL, 1959, the author was sent by the South Pacific Commission to the countries of Sierra Leone and Nigeria, West Africa, to conduct an investigation of the natural enemies of the various species of *Oryctes* (Coleoptera, Scarabaeidae, Dynastinae) occurring there. The object of this study was to find and introduce to the islands of the South Pacific suitable parasites and predators of these beetles in order to establish a biological control over the introduced *Oryctes rhinoceros* Linn. which has become a serious pest of coconut palms in the area.

In Sierra Leone and Nigeria, coconut palms are confined mostly to village sites; the groves are from 15 to 50 palms, depending on the size of the village. Because of this, nearly all the work was carried out on oil palms (*Elaeis guineensis* Jacq.) which, together with the *Raphia* palms of the swamps, are the most important hosts of the species of *Oryctes* found. The oil palms occur in an extensive belt that follows the coast of West Africa and extends inland nearly 100 miles in some places.

There are two distinct climatic seasons in West Africa, and these greatly affect the insect populations. The wet season begins generally at the end of April and lasts until sometime in September. By the end of November the dry season has set in, and from then until April little or no rain falls. At times the rains will cease in August and commence again in September, but during 1960 this type of rainfall did not occur in Nigeria.

Insect activity begins with the coming of the rains in April or May and gradually ends in November or December. There are, of course, many exceptions to this; some species seem to be found only during the dry season and others congregate along streams and in swamps, giving a false impression of their absence.

During the dry season in Sierra Leone and in parts of Nigeria, it is the practice to burn off the bush to clear the land for planting. The oil palms in these areas are usually not affected by the fires, and the larvae of *Oryctes* and other beetles within the standing rotten trunks are not harmed.

The low-lying land of the southern part of eastern Nigeria is divided by numerous slow-moving streams which give rise to large swampy areas as they wind their way towards the sea. Because of this and the heavy rainfall, extensive burning is not possible. In the swamps are dense stands of *Raphia* palms which flower and die, providing a continuous supply of breeding sites for *Oryctes*. The higher ground between the streams and swamps supports large stands of oil palms, both cultivated and wild, from which come the main export of the area in the form of palm oil and kernels.

PREDATORS AND PARASITES ENCOUNTERED

Neochryopus savagei Hope (Coleoptera, Caraboidea, Scaritidae)

The large scaritid beetle *Neochryopus savagei* was first found in *Raphia* palms growing in the swamps at Umudike, near Umuahia, eastern Nigeria. In April, 1960, an adult beetle of this species was found inside a standing rotten *Raphia* palm trunk where it was actually engaged in feeding on a larva of *Oryctes obausi* Minck. A search of other rotten palm trunks in this area turned up two large larvae of *Neochryopus*. Afterwards, additional adult specimens were recovered from the debris which normally collects in the old dead leaf bases just below the crowns of oil palms left by workers engaged in cutting the bunches of fruit in a grove of palms on the Agricultural Station. This accumulation of rotten organic matter provides a breeding site for *Oryctes sjostedti* Koble, and *Neochryopus* breeds here and preys on these dynastid grubs.

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Data obtained from the examination of field-collected larvae of *N. savagei* indicated that there were five instars. The length of the fourth instar period of a single larva provided with a constant supply of small cetoniid and *Oryctes* grubs was slightly over 2 weeks. The pupal period was 10 days. Several of these scaritid larvae lived 3 weeks without food. Considerable difficulty was experienced in hatching the eggs laid by captive adult beetles and rearing their larvae in the laboratory because both stages were frequently attacked by fungus. In the case of the larvae this fungus appeared to be a *Metarhizium*.

The adult beetles mated readily in small cigarette tins (14 cubic inches in capacity), which were partly filled with moist rotten palm fiber. The eggs of these scaritids were found in the medium, there being one egg per beetle. In a single instance a second egg was laid 3 days after the first had been discovered. The eggs were oval in shape, about 2 mm long and 1/2 mm wide. When laid they were sticky, and quickly became covered with bits of frass. This made them hard to find and, as no special attempts were made to discover them, no doubt many were missed. Adult female beetles which were dissected contained a maximum of four large eggs.

Both the adults and larvae of *N. savagei* readily attacked, killed, and consumed cetoniid, *Oryctes*, and other dynastid grubs of a size up to 10 g in weight (the size of an early third instar *Oryctes* larva). The larvae of the palm weevil, *Rhynchophorus phoenicis* F., were offered to the adult beetles and while these were usually killed, the beetles did not seem to feed on them to any extent.

The adult scaritids survived for long periods without food, the maximum period noted being about 4 weeks.

The adult beetles are winged and are strong fliers. Occasionally they are attracted to lights at night.

The sexes are readily distinguishable. The mandibles of the male are elongated, and the distal portion is without well-developed horizontal teeth. Those of the female are slightly broader and shorter, and the left mandible has a broad, flattish, horizontal inner tooth which forms a subapical notch. The mandibles of the

males are apparently adapted for grasping the female around the back of the head during copulation. However, both sexes feed readily on scarabaeid grubs.

The sex ratio was found to be 1 to 1. Usually one or two adult beetles were found in the debris of an oil palm, but on one occasion four were taken in a single site. No figures were obtained on the sexes collected from individual palms; the ratios were calculated from total field collections.

The majority of the beetles were collected from the oil palm debris; however, a fairly large number of both adults and larvae were also found in the rotten *Raphia* trunks. The fauna of the oil palm trash and of the standing rotten trunks was, with one exception, identical. The exception was *Oryctes sjöstedti*, which was only found breeding in the oil palms. However, it seems safe to regard this site as a sort of elevated trash heap rather than an unique environment.

At Umudike the beetles were kept in round, 50-cigarette-size tins. At first only one adult was put in each tin, but later, to conserve space, two were placed in each container. Rotten palm fibre was added to each tin to give the beetles something in which to dig. After about 1,400 specimens had been collected at Umudike, they were taken to Ibadan and there packed for shipment. Plywood trays divided by partitions into 2-inch cubes were used to hold the beetles in transit. Each cube was partly filled with moist wood wool. A single scaritid was placed in each compartment, and the tray was covered with 1/8-inch-mesh wire screen held down with staples. Three or more trays were then packed into a heavy polythene bag to prevent loss of moisture. The trays in their bags were packed into heavy cardboard boxes which were wrapped with paper. From 4 to 6 boxes made up a shipment. The insects were sent from the Ikeja airport via Paris to Fiji by air freight. Cigarette tins were used as containers for the first two or three shipments, but these were heavier than the plywood trays.

During the shipments, there were always more beetles than containers. Usually, enough males were discarded to bring the sex ratio to 1 male to 3 females instead of the normal 1 to 1. An ideal container would have been an alumi-

num box of about 8 cubic inches capacity, and had these been available in quantity many more insects could have been sent.

An attempt was made to keep *N. savagei* adults together in a large tin, but this was unsuccessful due to cannibalism even when 8 cubic inches were allowed per beetle.

At first it was thought desirable to provide food for the insects during the time they were held in Nigeria. Later it was found that they fared much better if they were not fed. The grubs put into the tins were only partly consumed, and the rotting remains in the small containers evidently created a most unfavorable environment.

Dorylus (Anomma) nigricans Ill. (Hymenoptera, Formicidae, Dorylinae)

Throughout the search for parasites and predators of *Oryctes* in West Africa it was noted that the larvae of the rhinoceros beetles occurred in large numbers in standing rotten palm trunks but not in fallen logs. In Sierra Leone this situation was often observed, but no experiments were made to determine why the fallen logs were not used by the beetles. It was thought that possibly the principal species encountered, *Oryctes owariensis* Beauv., unlike other members of the genus, did not favour such sites.

On Moor Plantation, Ibadan, Nigeria, an experimental grove of coconut palms was found to be infested by a fair number of *Oryctes monoceros* Ol. This species was found breeding inside the bases of old coconut palm stumps and in standing rotten coconut trunks, the products of several severe lightning strikes in the grove. However, in the numerous rotten trunks which had been felled, there were no *Oryctes* larvae nor, for that matter, any larvae of any of the numerous species of cetonids and small dynastids which usually occur with *Oryctes* in West Africa. There were clear signs that, before the trunks had been felled, a considerable amount of breeding by *Oryctes* had taken place within them. It was also noted that the hollowed interiors of these fallen trunks contained much less frass than would have been expected.

Specimens of adult rhinoceros beetles from this grove were sent to the British Museum (Natural History) with a request that they be

compared with specimens of *Oryctes monoceros* from East Africa. This was done, and the Ibadan species was found to be identical with the East African *O. monoceros*.

To determine whether the fallen trunks were suitable as breeding sites, four sections were selected and set upright. After these had been in position for about 3 weeks, they were split open. Seven adult beetles of *O. monoceros* and 14 eggs were collected from them.

Five sections of the fallen trunks were carefully split lengthwise, and new hollows were either carved out by hand or the existing hollows were utilized. These prepared sections were stocked with *Oryctes* larvae, and frass was packed into the hollows around them. The two halves were then brought together and fastened in place with bands of wire. Some sections were left lying on the ground, others were raised slightly at one end. In addition to the logs, a sawdust pile was established and stocked with larvae of *O. boas* F. and a few *O. owariensis*. For all of these trials only third-instar larvae were available.

The following events took place:

1. 15 November 1959. One log was entered, and the larvae were eaten by a small greyish rat.

2. 30 November 1959. All the logs were entered, the frass was removed, and the larvae were eaten by a swarm of "driver" ants, *Dorylus (Anomma) nigricans*.

3. 14 December 1959. The logs, having been restocked with *Oryctes* larvae, were again entered, the frass was removed, and the larvae were eaten by a very large swarm of "driver" ants, *Dorylus (Anomma) nigricans*. The sawdust pile was also entered by the ants and about one-third of the grubs was eaten.

4. 10 January 1960. Additional logs were added on 3, 4 January and a small section of log which could be moved about with ease was prepared. This was placed in the dry bed of a stream, about 50 m distant, where "driver" ants had been observed. On the evening of 10 January the ants invaded this log and also entered all the other logs in the experimental area. One of these logs was constructed so that the larvae were in a central frass-packed hollow which had no openings at either end. The only means of access to this hollow were the holes left in the

trunk by the workings of xylocopid bees, a natural feature of all of the rotten logs in the grove. The ants entered through these holes, removed the frass, and ate the *Oryctes* larvae, leaving only the head capsules.

5. 11 January 1960. The logs which had been invaded by the "driver" ants on the night of the 10th were broken up to determine if any of the *Oryctes* larvae had escaped. In three of the logs in the upper breeding site experimental area a few intact larvae and pupae were found, but in the log located in the stream bed nothing remained. The following results were obtained from the logs in the upper area: One log which had been stocked with 7 larvae contained 1 living larva and 1 pupa; one log which had been stocked with 10 larvae contained 2 living larvae and 1 pupa; one log with no access from either end which had been stocked with 6 larvae contained 1 living larva and 1 pupa.

The area was visited daily and the logs were inspected at intervals of 4 to 5 days to determine if the larvae were alive. The last stocking of the logs with larvae was on 16 December 1959.

In November, the end of the wet season in Nigeria, the ants were active throughout the area. However, after the end of the rains the ants moved into stream beds; by January, only invasions of short duration were made into nearby areas.

The invasion of the experimental site on 30 November lasted about 14 hr. The last sortie on 10 January was only about 7 hr long.

Another species of *Dorylus* (*Anomma*) was found in the coconut grove; this ant was never observed to enter the logs. No attempts were made by either species of *Dorylus* (*Anomma*) to enter the tops of the stumps or to climb up the standing trunks. The ants were able to climb vertical surfaces but did not seem to do any work, such as removing frass, while on them. When *D. nigricans* entered the rotten logs, they did so by choosing holes which were more or less horizontal. They always used these holes to bring out the frass from the interior.

Ochryopus gigas Schio. (Coleoptera, Caraboidea, Scaritidae)

Occasionally the very large scaritid *Ochryopus gigas* was found both in the debris accumulated

below the crowns of oil palms and in standing rotten palm trunks. During April and May, 1960, adults of this species were taken around lights at night. However, this species was never found to be common and its larva was not discovered. In the laboratory *O. gigas* attacked, killed, and consumed both larvae and adults of *Oryctes*.

Scolia sp. (Hymenoptera, Scoliidae)

In the oil palm debris and in rotten *Raphia* trunks large *Scolia* cocoons were frequently found. Many of those taken from these sites had already hatched. Sometimes the head capsule of the host grub would be found entangled in the silk of the cocoon, and from this it was determined to be parasitic on *Oryctes ohausi* and *O. sjöstedti*.

The adult wasps were never observed in the field, but two males and two females were bred out in the laboratory. The female specimens were sent to the British Museum (Natural History), where they were identified only as *Scolia* sp., "not in British Museum collection."

Judging from the number of empty cocoons, this parasite was thought to be rather common, but large-scale collecting efforts resulted in only about 65, nearly half of which contained dead pupae. Nevertheless, the cocoons were sent to Fiji where an attempt was made to rear the wasps. Unfortunately, this has proved unsuccessful, and the wasps which did hatch died in the laboratory.

OTHER PREDATORS AND PARASITES

1. *Alaus* ? sp., *Calais* sp. (Coleoptera, Elateridae)
2. *Morio guineensis* Imh. (Coleoptera, Caraboidea, Carabidae)
3. Genus ?, species ? (Diptera, Tachinidae)
4. *Platymerus biguttata* Stål (Hemiptera, Reduviidae)
5. Genus? species? (Diptera, Tabanidae)
6. Genus? species? (Araneida, Aviculariidae)

1. Large elaterid larvae were found inside the standing rotten oil palm trunks in close proximity to *Oryctes* larvae in both Sierra Leone and

Nigeria. They were never common, and in Sierra Leone only 24 were collected from over 500 rotten oil palm trunks. Specimens were determined at the British Museum to be perhaps a species of *Alaus*.

A smaller elaterid larva found in a rotten oil palm was reared on *Oryctes* and cetoniid larvae, the adult beetle being identified as *Calais* sp.

2. Occasionally larvae and adults of a small carabid beetle, *Morio guineensis*, were found in the frass in the rotten palm trunks. In the laboratory these readily consumed first instar *Oryctes* larvae.

3. Large numbers of the larvae of *Oryctes boas* F., collected from a manure heap on the farm of the University College, Ibadan, were reared in captivity. These were dissected whenever they showed signs that something was wrong with them. One, a prepupal stage larva, died suddenly and was cut open. In the abdomen was a very large larva of a tachinid fly which had also perished. Following this discovery, some 1,000 *Oryctes boas* grubs were collected from this manure heap, but no other parasites were recovered.

4. Neanides and adults of the large reduviid, *Platyerus biguttata*, were found fairly frequently in the open hollow tops of the standing rotten oil palm trunks in Sierra Leone during April, May, and June. Laboratory trials were conducted to see if this bug would prey on adult *Oryctes owariensis*, but without result. Even adults which had been held without food for nearly 2 weeks showed no interest in this large rhinoceros beetle. During May and June, 1959, *Platyerus biguttata* came to lights at night on several occasions. No other Coleoptera than *Oryctes owariensis* were tried as prey for this reduviid.²

5. In a standing rotten coconut palm trunk on Moor Plantation, Ibadan, three tabanid larvae

were found in the frass along with the grubs of *Oryctes monoceros*. These readily attacked and killed young scarabaeid larvae in captivity. A week or so later all three pupated and after 2 weeks the adult flies emerged. Unfortunately, the specimens sent to the British Museum were badly broken in transit and were not able to be identified. The tabanids were bright orange with a large purple band across each wing.

6. In Sierra Leone, both inside the hollow tops of standing rotten oil palm trunks and in the crowns of living oil palms, a large aviculariid spider was frequently encountered. This fear-some-looking arachnid evidently attacked the oil palm climbers, who had their own remedy for the effects of its bite. Experiments were made to see if this spider would kill adult *Oryctes owariensis*, but the results were negative.

In Nigeria this palm tarantula seemed to be unknown to the people and no specimens were found.

Coleolaelaps sp. (Acarina, Laelaptidae)

Several investigators have reported that mites feed on the eggs of *Oryctes*. Venkatraman reported a *Coleolaelaps* sp. which "apparently fed on *Oryctes* eggs" in Ceylon. Surany reported several instances of mites feeding on *Oryctes* eggs and stated that they were important under certain circumstances in its control. Unfortunately, Surany did not identify the mite in question in his report.³

Clusters of mites around eggs of *Oryctes owariensis* were frequently observed in Sierra Leone from June onward throughout the rainy season in 1959. These mites were found on eggs enclosed in balls of frass formed by the adult beetles as they oviposited in the rotten wood inside the standing rotten oil palm trunks. It was noted at the time that eggs which had mites on them never hatched, while eggs in the vicinity without mites hatched readily. These mites were collected and sent to the British Museum where they were identified as *Coleolaelaps* sp.

Adult mites of this species were common on the larvae of *Oryctes owariensis*, *O. boas*, and *O. monoceros*, but were encountered only rarely on the adult beetles.

² The author is at present engaged in a study of the allied species, *Platyerus rhadamanthus* Gerst., which does attack the adults of *Oryctes monoceros* Ol. However, old adults which have accumulated large fat deposits usually refuse to attack anything. At the time *Platyerus biguttata* was investigated it was not known that the fifth-instar neanides would also attack adult rhinoceros beetles and, perhaps because of their more rapid metabolism, are generally easier subjects with which to work.

³ *Diseases and Biological Control in Rhinoceros Beetles*. South Pacif. Com. Tech. Pap. 128. 1960.

In Nigeria, *Coleolaelaps* was again found on the eggs of *Oryctes boas* in March, 1960, following a few early rains. The *Oryctes* eggs were taken in a large manure heap on the farm of the University College, Ibadan. Mite-infested eggs were collected and placed for observation in covered shallow glass dishes filled with a manure and frass mixture. At the same time newly laid eggs were obtained from captive specimens of *Oryctes boas*. Mite eggs and immature and adult mites were transferred from the originally infested, field-collected eggs to the newly laid eggs and to uninfested, field-collected eggs.

It was noted that *Oryctes* eggs which had mites or mite eggs on them were all slightly discoloured and at times showed brownish spots.

When mite eggs were transferred to non-discoloured, field-collected eggs, or to newly laid eggs, the mites hatched and in a short time made their way throughout the medium to the original egg from which they had been transferred. Here they gathered and fed on the yolk of the now partly collapsed egg.

The adult *Coleolaelaps* were never observed to feed on either nondiscoloured, field-collected eggs or on the newly laid eggs, but they fed readily on the discoloured ones and on a non-discoloured egg which was punctured with a needle.

None of the discoloured eggs hatched and, with the exception of the punctured, nondiscoloured egg, both newly laid and field-collected ones produced normal larvae.

No further tests were carried out with *Coleolaelaps* due to the discovery of other predators which appeared to be more promising.

OTHER MITES ASSOCIATED WITH *Oryctes*

In all, some 14 species of mites (Acarina, Uropodina, and Canestrinidae) were found associated with the larvae and adults of *Oryctes* in Nigeria. Two of these, a canestriniid and a species of the Uropodina, were found commonly on the adults of *Oryctes monoceros* and *O. owariensis*. The canestriniid was found in large numbers on the first three abdominal tergites beneath the elytra. The uropodinid was taken wandering about both on the venter of the

beetle and under the wing cases. At times both species of mites were found heavily infested with a fungus resembling closely some of the Laboulbeniales. The fungus did not appear to harm them, and gravid females were frequently observed to produce normal eggs in spite of heavy infestations.

The species of Uropodina found on *Oryctes* was also collected in numbers from the adults of *Neochryopus savagei*.

SPECIES OF *Oryctes* ENCOUNTERED (Coleoptera, Scarabaeidae, Dynastinae)

1. *Oryctes monoceros* Olivier

Both in Sierra Leone and in Nigeria *Oryctes monoceros* was always found in places where there were coconut palms in the immediate vicinity. On Moor Plantation, Ibadan, this species was taken breeding in standing rotten coconut trunks and in the bases of coconut stumps. With the exception of Moor Plantation, however, *O. monoceros* was rare in all of the places visited.

2. *Oryctes boas* Fabricius

In Sierra Leone *Oryctes boas* was commonly encountered breeding in village compost heaps, but in similar sites in Nigeria it was rare. However, in Nigeria a large manure pile was found at the farm of the University College, Ibadan, in which there were thousands of larvae, pupae, and adults of this species. In March and early April numerous adults and eggs were found in this site, but at other times mainly larvae of various instars were present. These findings seemed to indicate that, while there was some overlap of generations, nevertheless there was a definite yearly cycle.

Recently an experimental planting of oil palms in Northern Nigeria was reported to be rather severely attacked by an *Oryctes*, and specimens extracted from the crowns of these palms proved to be *O. boas*.

3. *Oryctes owariensis* Palisot de Beauvois

Oryctes owariensis is a large species, the well-developed adults being larger than the other *Oryctes* species in West Africa and larger than *O. rhinoceros* of Southeast Asia and the Pacific

region. Probably because of its size, the species has been confused with *O. gigas* of Madagascar.

Oryctes owariensis breeds, as far as is known, only in rotten wood and prefers rotten palm logs. It was found commonly in Sierra Leone and Nigeria in standing rotten oil palm trunks, standing rotten coconut trunks, and in rotten *Raphia* palm trunks. Usually this was the only species of *Oryctes* present in these sites, but sometimes the larvae of *O. monoceros* or *O. ohausi* occurred with it. In Sierra Leone an adult specimen was extracted from the crown of an oil palm. Observations in both Sierra Leone and Nigeria seemed to indicate that this beetle did not prefer coconut palms as a host plant.

4. *Oryctes sjöstedti* Kolbe

As has been stated previously, this species was only taken breeding in the debris accumulated in the dead leaf bases just below the crowns of oil palms. In this site the maximum number of larvae found was six, all third instars. Pupae were not infrequently encountered, usually in a cavity within one of the old leaf bases; the adult beetles were also found both within these and in the debris enclosed by them. Adults were taken at mercury vapour lights fairly frequently, but never in numbers; one or two per night was the largest catch. This species was most common at Benin, Nigeria, on the West African Institute for Oil Palm Research station and at Umudike in eastern Nigeria.

5. *Oryctes ohausi* Minck

Perhaps this species has been confused with *O. monoceros* in the past; anyway when specimens were sent to the British Museum for determination, it was surprising to learn that no examples of this species were in the collection. *O. ohausi* was commonly found breeding in the standing rotten trunks of *Raphia* palms. Adults, larvae, and pupae were found in fair numbers in these sites, and not infrequently in company with *O. owariensis*. There was an average of eight larvae per trunk during April, 1960, at Umudike in eastern Nigeria. A single adult male was taken in a rotten oil palm stump on Moor Plantation at Ibadan.

6. *Oryctes erebus* Burmeister

This species has been recorded a number of times from West Africa but was not found during this investigation.

NOTES CONCERNING ADULTS OF *Oryctes*

All of the investigations conducted in West Africa on the adults of the various species of *Oryctes* were carried out with the objective of finding parasites of the mature beetles.

The main difficulty in searching for parasites of the adults is to get large numbers of beetles which have been exposed in nature. When mature beetles are taken from rotten logs, a fairly high proportion of them are recently emerged and have never been outside the breeding site. If *Oryctes* flew readily to lights, the problem would be simple. However, it is not particularly attracted by light, although recently some success has been reported with a special ultra-violet lamp used in the Pacific.

In Western Samoa split logs laid flat on the ground are used to trap adult rhinoceros beetles. Each trap consists of four to eight logs each about 4 ft long. A similar type of trap was tried in Nigeria without success.

Another type of rotten log trap was devised which gave fairly good results in Nigeria. This was made of a foot-long section of coconut trunk through which a hole was bored from end to end. This section was placed on top of a No. 10 can which was either sunk into or rested on a coconut stump. The beetles landed on the top of the log, crawled down the hole and fell into the can underneath. The trap caught quite a few *Oryctes monoceros*, the largest single catch being three.

Efforts were made to use captive beetles to attract others. No positive results were obtained along this line, but it was found that *O. owariensis* had two distinct flight times, one in the evening and the other in the early morning. Furthermore, beetles which did not fly in the evening flew in the morning, and beetles which did fly after sundown did not fly later on.

No parasites were found in the adults of *Oryctes*, but the numbers examined were probably not high enough to give any reasonable hope of success.

DISCUSSION AND CONCLUSIONS

In both Sierra Leone and western Nigeria predators and parasites of *Oryctes* larvae were not at all common. The only controlling factor of this nature seemed to be periodic invasions of the fallen logs by "driver" ants. Standing rotten palm trunks contained large numbers of *Oryctes* in all stages of development. It should not be supposed, however, that there were normally large numbers of these breeding sites in any one small area. Further, not all of the trunks contained *Oryctes*. It was noted that rotten trunks with long black fibers in their interiors seldom supported anything at all. Perhaps the form of decay, fungal or bacterial, made these unattractive to the beetles.

In areas like one reported in western Nigeria where an old oil palm plantation had been poisoned off and the dead palms left standing, serious damage was caused to the young palms planted between them by *Oryctes*, which bred in the rotten trunks.

Parasites and predators were found readily only in the regions of the deltas of the Niger

and Cross rivers of eastern Nigeria. While the same species of these are wide-spread throughout West Africa, they were common in this particular area. It is thought that the practice of burning off the bush, which is done on a large scale in western Nigeria and Sierra Leone, plays an important role in limiting the numbers of predators and parasites. The land of the delta areas is too swampy for burning. *Oryctes* is not affected by bush fires on account of its habits.

It is, of course, logical to assume that the long dry season, together with the absence of numerous streams and swamps, probably also plays a major role in limiting populations of parasites and predators which have fairly short life cycles. No doubt it does, but this and burning complement each other, and it is difficult to say which is the more important.

Under West African conditions it appears that many of the populations of *Oryctes* are limited by the number of available and suitable breeding sites, and that their predators and parasites are limited by unfavorable environmental conditions which are determined largely by cultural practices and climatic conditions.

Characteristic Features of the Volcanism of the Siberian Platform

V. S. SOBOLEV¹

WIDESPREAD VOLCANISM is characteristic of the Siberian platform, and was especially intense during uppermost Paleozoic and lower Mesozoic time. The Siberian traps, which occupy an area of more than 1,500,000 km², are best developed there. These are effusive and hypabyssal rocks of basalt-dolerite type, closely resembling trap rocks in other parts of the globe, especially the Karroo dolerites of South Africa.

The rise of trap magma began in the upper Paleozoic (Permian or even as early as Upper Carboniferous) time, and reached its climax in the Lower Triassic period. It was accompanied by the ejection of much pyroclastic material, which formed a thick series of tuffs. Lava sheets and hypabyssal intrusions of various kinds and sizes were formed.

The process of volcanism was rather complicated, and at present M. L. Lurie and V. Z. Masaitis distinguish five volcanic phases and 13 separate intrusive complexes, each having its own specific features and pattern of development in various parts of the platform. In spite of this, however, the magma had some characteristic features over the entire area, notably an iron content somewhat higher than is usual and an especially rapid increase of relative iron content during the process of crystallization differentiation. The increase of the iron content of the femic minerals in the process of crystallization prevails over the conventional reaction series of Bowen. For example, olivine of early formation contains about 20% fayalite, that characteristic of the usual type of traps contains about 40% fayalite, and the iron content of olivine in pegmatoid veins is as high as 80%.

The residue of the differentiation is as a rule micropegmatite, either in the mesostasis, or in some cases forming veinlets of granite compo-

sition. However, such veinlets are quantitatively very small. Much rarer is the formation of alkaline rocks, such as teschenite, in the last stages of differentiation.

The above characteristics of crystallization differentiation (rapid change of the iron content of femic minerals and the subordinate role of the discontinuous reaction series) are typical not only of the trap formations, but also of the deeper-seated magmatic complexes of the platform. The gabbro-anorthosite-granite complex of the margin of the Russian platform, with its characteristic granites of Rapakivi type, belongs to this group. These characteristic features distinguish complexes of this type from the typical granodiorite complexes of orogenic zones, in which crystallization largely corresponds to the well-known Bowen series. Relative increase of the iron content of femic minerals is there much slower, as is clearly seen by comparing it with the change in plagioclase composition.

Along with the trap formation, in part simultaneously and in part a little later, another type of volcanism developed widely on the margin of the platform, with the formation of ultrabasic and alkaline rocks. Differentiated effusive and intrusive complexes were formed in some regions, kimberlites in others.

A typical example of the differentiated complexes can be seen in the northern part of the Siberian platform in the area of the so-called Gulinski intrusion. The effusives range from meimechite, the closest extrusive analogue of true intrusive ultrabasic, to different kinds of alkaline basaltoids containing nepheline and plagioclase. Among the intrusives are all kinds of rocks from dunite to various alkaline rocks rich in nepheline. Carbonatite is also present. E. L. Butakova (1956) and Y. M. Sheinman (1955) have shown that the volcanic rock formation here was largely simultaneous with erup-

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tion of the trap magma. There are traps both older and younger than the alkaline rocks.

Kimberlite has been formed extensively in the northeastern border of the platform, more than 100 pipes and dikes being known there at present. For some kimberlite bodies the same sort of relationship to the traps has been established as for the alkaline basaltoids. Some of the kimberlite is not younger than Permian in age, since pyrope and diamonds from it occur in the Upper Permian deposits. However, there undoubtedly are younger kimberlites also, for a fragment of a belemnite of Upper Jurassic or Lower Cretaceous age was found in one of the pipes.

Kimberlite, as a magmatic rock, belongs to the ultrabasic group, its composition ranging from a form nearly devoid of alumina and alkalis to one rather high in Al_2O_3 and especially high in K_2O in mica-rich varieties. The principal mineral is always olivine, containing up to 10% Fe_2SiO_4 , and is present in at least two generations: large crystals, commonly partly resorbed, and small idiomorphic microphenocrysts. Phlogopite occurs in idiomorphic plates and ranges widely in quantity. It is unquestionably magmatic. Pseudomorphs of pyroxene microlites are sometimes seen in the vitreous matrix. The latter is always altered. In the northern regions fine-grained monticellite has been found in kimberlite for the first time, chiefly in dikes. Nepheline also is supposed to be present. Pyrope, and probably picroilmenite and chrome spinel, commonly belong to the first generation of phenocrysts. Perovskite is a later accessory.

As in South Africa, the kimberlite has a brecciated structure and is contaminated by fragments of various sorts of rocks. There are, on the one hand, typical pyroclastic rocks filling explosion pipes, and, on the other, magmatic breccias with various contents of xenoliths. Since the rocks have been altered (serpentinized and carbonatized), it is not always possible to prove the presence of magmatic cement.

The fragments of other rocks may be subdivided into:

- 1) Fragments of ultrabasites and eclogites whose origin is in some way connected with the origin of the kimberlite itself;

- 2) Fragments of rocks picked up by the

magma from (a) the crystalline basement formations, and (b) the sedimentary cover.

Fragments of the first type include various ultrabasites—olivinites, peridotites, and others—often containing pyrope as well as typical eclogites. The discovery of diamond-bearing eclogites, resembling the well-known eclogite xenolith found by Bonney (1899) in South Africa, is of particular interest. Together with such eclogites brought up from great depth, there are eclogites and eclogite-like rocks (containing plagioclase) picked up from the crystalline basement and formed by eclogitization of hypersthene schists.

The fragments of rocks picked up by the magma vary widely in quantity and composition. Xenoliths of gneisses and schists are abundant in several of the pipes. This can be taken as proof that the "explosion" that formed the pipe took place at a level lower than the base of the sedimentary cover. Allowing for this, and taking into consideration the geophysical data on the depth of the crystalline basement in the area and also the thickness of the rocks since removed by erosion, we can say that the explosion took place at a depth somewhere between 2 and 4 km. The depth is greater than in the case of the formation of the trap necks, which was 0.5 to 1 km.

As in South Africa, xenoliths of rock formations that occur at much higher levels (sometimes several hundred meters higher) are found among the fragments, proving that there was not only an ascending but also a descending movement of the material in the pipe.

The synchronicity of their formation has led to the hypothesis of a genetic connection between the ultrabasic rocks and kimberlites and the trap magma of the Siberian platform. Petrographic data, however, do not support this hypothesis. The olivine of the kimberlites and the meimechites contains only 10% fayalite, and this is proof enough that these rocks could not have originated as a result of differentiation of the trap magma. The author quite agrees with Y. M. Sheinman's (1955) suggestion of the formation, in this case, of magmatic chambers at much deeper levels than those of the trap magma.

The development of trap volcanism on such

an enormous scale leads us to the conclusion that regional melting of the basalt layer took place here, probably in its upper part. However, nowhere in the platform did the magma chambers reach the sialic shell, and the small granitoid veinlets were formed wholly as a result of local crystallization differentiation. Taking into consideration the existing data on the structure of the earth's crust in the platform, the depth of such magma chambers appears to have been about 25 km, and the geothermal gradient at the time of volcanism appears to have reached 40 C per kilometer.

Some differences in composition of the traps might have resulted from differences in depth of the magma chambers in different parts of the platform and resultant differences in the differentiation phenomena.

The presence of effusives of ultrabasic composition (meimechites, kimberlites) is definite proof of the existence of a corresponding magma. This magma could be formed only by the remelting of ultrabasic rocks, which in turn is proof of the existence of rocks of corresponding compositions below the Mohorovicic discontinuity.

In the case of the formation of differentiated complexes, there is no doubt of the presence of big magma chambers and a relatively slow rise of magma either to the earth's surface or to the corresponding intrusion chambers. A complicated evolution of the rocks takes place as a result of involvement of the higher levels of the earth's crust in melting and, perhaps, as a result of assimilation and differentiation.

In the case of the kimberlites the quantity of rising magma is very small. This can hardly be the result of the low penetrability of the earth's crust. Rather, it is a proof of the formation of very small magma chambers in which remelting was partial, and a magma which rose very rapidly up the deep fissures containing many suspended crystals that formed not only as a result of crystallization in the chamber but also that remained as a result of the partial melting.

Not only theoretical calculations but also experimental data now show that if diamonds were formed at a temperature of about 1200 C, the pressure must have been more than 40 kilobars. The notion that diamonds were brought

by the magma from great depth, and not formed at the time of explosions near the earth's surface, can be considered valid. Sometimes, on the basis of the above data, an attempt is made to determine the depth of the magma chamber from the implied hydrostatic pressure of the overlying rocks. This approach we cannot agree with, since the pressure in the earth's crust, within the zone of metamorphism, can be as high as 15 kilobars, which is several times the pressure resulting from load at that depth, the difference between the pressure at the time of the mineral formation and the calculated pressure due to the load being as much as 10 kilobars. Such zones of higher pressure may extend into the depths of the mantle, and it is to them that the regions of kimberlite development are likely to have belonged. The depth of formation of the magma chambers, in this case, may be less than calculated—that is, not 150 km but 70 to 100 km. As a result, when magma rises to a higher level, pressure still remains high, though it falls by a quantity corresponding to the weight of the vertical column of magma. In places at a depth of 3–4 km (see above), a breaking of the earth's crust occurred, accompanied by the formation of peculiar pipes and a sudden pressure decrease, constituting a kind of explosion. A great quantity of pyroclastic and xenogenic material rushed into the pipe, part of it being thrown up and then sucked back into the pipe again. The fragments filling the pipe may later be cemented by the rising magma.

The pressure before the explosion is not only below that shown by the equilibrium curve of diamonds but also below that shown by the curve of pyrope, since the kelyphite rims around grains of the latter must have formed before the explosion. The fact that the diamonds are neither completely resorbed nor graphitized is due to the rapid rise of the magma and its comparatively low temperature. The temperature of the magma must be lower than that shown by a curve corresponding to the region of metastable existence of diamonds (V. Sobolev, 1960), which begins at 1200 C at normal surface pressure and rises to 2200 C at 30 kilobars. As is known, the diamonds show only traces of graphitization, which appear as graphitic rosettes near some inclusions.

Recently, in connection with the discussion of the composition of the subcrustal substratum, great attention is once more being paid to the eclogite problem. The suggestion has been made (Fermor, 1914; Lovering, 1958) that the substratum below the Mohorovicic discontinuity is eclogite. Some authors are of the opinion that this eclogite layer extends to a depth of 900 km (V. V. Belousov, 1960), i.e., to the base of the Galitzin layer. The only valid data available for discussion of this matter have been derived from study of the kimberlites—a fact that makes it desirable to treat this problem here.

As is known, a great quantity of xenoliths of ultrabasic rocks, in some cases directly related to eclogites, are to be found in many kimberlite pipes. This fact suggests that such xenoliths are at least in part the remains of the partially-melted substratum, the more so as the composition of the olivine in them resembles that of the first-generation olivine of the kimberlites. The question is, however, still open to discussion. There is some probability that these rocks were picked up by the kimberlites during their rise toward the surface, not only in the substratum but also at much higher levels. The ultrabasic magma chambers are likely to have revived several times, and the formation of ultrabasic intrusions may have taken place during the first stages, further intrusions taking place later with the rapid movement of new portions of magma in new geologic conditions. Such intrusive massifs could have consisted of pyrope peridotite, such as that in Czechoslovakia.

The absence of diamonds (at least in appreciable quantity) in the ultrabasic xenoliths speaks against the supposition that the xenoliths were brought directly from the deep magma chamber. Although the presence of diamonds in pyrope peridotites has been asserted by some workers, neither a xenolith with a diamond, nor its photograph, nor a detailed description of it, can be found anywhere. Many attempts to obtain diamonds by grinding and concentration of considerable quantities of ultrabasic xenoliths and eclogites have resulted in failure. This fact, however, cannot altogether disprove the hypothesis of the subcrustal origin of these rocks, since the distribution of diamonds in the substratum may be nonuniform. Also, they may have, for the

most part, crystallized directly with the formation of kimberlite magma.

On the other hand, two findings of diamond-bearing eclogites, which are subject to no doubt and have been described in detail, are proof of the existence of subcrustal eclogites. Diamond formation in the zone of metamorphism is impossible. The pressure there has never reached even that of coesite crystallization, which is lower than that of diamond formation. It is interesting to point out that the Jakutian diamond-bearing eclogite in its ratio of FeO to MgO is nearer to basic rocks than to ultrabasic rocks; it undoubtedly was not brought directly from the deep magma chamber, but was picked up from higher levels in the substratum.

Comparing all the above-mentioned data, we come to the following conclusions regarding the constitution of the upper mantle and its relationship to the earth's crust:

1. At comparatively small depths, probably less than 50–70 km, the subcrustal substratum is of peridotite composition, corresponding approximately to the composition of meimechite or kimberlite, the latter being a magmatic rock.

2. In the region of kimberlite distribution, higher than the peridotite layer but below the Mohorovicic discontinuity, the substratum is eclogite with chemical composition very near that of basalt.

3. Pressures in the zone of metamorphism can vary greatly at one and the same depth, reaching at least 15 kilobars but never 20–25 kilobars.

4. There is some reason to believe that higher pressures are characteristic of large parts of the earth's crust, especially the border of the platforms. Pressure higher than simple hydrostatic pressure is also characteristic of the upper part of the subcrustal substratum in these same areas (probably down to a depth of about 150–200 km).

5. Higher pressure persisted in certain zones through considerable periods of geologic time, as is proved by the finding of ancient eclogitized schist in kimberlite of both Upper Paleozoic and Mesozoic age.

Examining the above statements, we come to the conclusion that the hypothesis of a subcrustal eclogite layer (Fermor, 1914) has been confirmed, but only in part. The author quite agrees

with the opinion of J. F. Lovering (1958), V. V. Belousov (1960*b*), and others, that a change of conditions (chiefly pressure, rather than temperature) leads to a shift of the Mohorovicic discontinuity, with the formation of eclogites at the expense of gabbroic rocks of the "basalt" layer. The total thickness of the basic layer, however, is probably not more than 30–50 km. Thus the eclogite layer is not to be found all over the globe, but only in the zones of higher pressure. In some cases, the basalt layer has been fully eclogitized and has entirely disappeared, and the sialic layer has come into direct contact with the Mohorovicic discontinuity. We can approach the problem of distribution of the subcrustal eclogite layer by comparing geophysical and geologic data: the distribution of kimberlite, the appearance of eclogite inclusions in effusives, and, partly, the distribution of rocks formed at high pressures in the zone of metamorphism, such as kyanite schists, eclogites, jadeite (taking into consideration possible changes over periods of time).

In the zones of normal or lower than normal pressure, the pressure of about 15 kilobars, which is necessary for the formation of eclogites, is reached at a depth of about 60 km, which is, as a rule, below the boundary separating the basic and ultrabasic rocks. Garnet peridotites, or some interlayers of eclogites that are close to ultrabasic rocks in composition, may be present there. In such cases the Mohorovicic discontinuity evidently corresponds to the true compositional border between the basalt and the peridotite layers, not to a phase transformation.

The isobar of the limit of possible diamond formation (40 kilobars) is, of course, well below that level. In the areas of normal or lower pressures, it must be below 120 km. In the author's opinion, the penetration of magma from such a depth is unlikely. Still less likely is the preservation of the diamond, even if magma chambers have formed at such depths.

In connection with this problem it is interesting to compare the data on the finding of diamonds in meteorites. As far as is known, diamonds have been discovered in stone meteorites of ureilite type (first in the Novourei meteorite) and in some iron meteorites. The author quite agrees with the opinion of Urey (1954, 1957)

that the presence of diamonds there is evidence of the formation of these meteorites by the breakdown of some celestial body, as big as the moon or bigger, in which the pressure was high enough for the formation of diamonds. Thus, we cannot agree with A. P. Vinogradov's (1959) opinion that achondrites were formed by the breakdown of small celestial bodies. The paragenetic associations characteristic of eclogites, and specifically pyrope itself, have not been found in the meteorites, however. This shows that in the basalt shell of the disintegrated body pressures nowhere reached 15 kilobars. This fact, together with the absence of meteorites of granitic composition, suggests that the body probably was smaller than the earth and less differentiated. This agrees with ideas which have already been developed on other grounds by A. N. Zavaritski (1943). The above-mentioned data do not, however, prove that all meteorites have had the same origin and resulted from the breakdown of one planet.

Various meteorites are still being searched for diamonds. This search is certainly of great interest, but there is little likelihood that diamonds will be found in other types of meteorites, particularly in chondrites. Without going into details on the hypotheses of the formation of chondrites, we are quite certain that in the later stages of existence of these meteorites the temperature was high enough so that diamonds would have turned into graphite even if they had existed. If, however, we should succeed in finding pseudomorphs of diamonds in chondrites, as we have in some iron meteorites, this would be a direct proof of the formation of chondrites by the breakdown of some big celestial body.

On the other hand, the discovery of graphite pseudomorphs of diamonds in iron meteorites shows that, after the breakdown of the parent planet, the temperatures of the meteorites were greater than 1200 C. The preservation of diamonds in the Canyon Diablo octahedrite suggests that the temperature of that meteorite at the time of the breakdown was below 1200 C, which means that it was not melted.

The general questions discussed here are, of course, still open to argument. Already, however, on the basis of available petrographic and min-

eralogic data, we can be more certain of the thermodynamic conditions in and the constitution of the upper mantle of the earth, and of the conditions of meteorite formation. The formation and alteration of diamonds are of particular importance in these considerations. There is no doubt that further mineralogic investigations in general, and the investigation of diamonds in particular, will open new approaches to the study of the composition of the earth and aid in penetrating the secrets of the solar system.

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Gibsmithia hawaiiensis gen. n. et sp. n.¹

MAXWELL S. DOTY²

ABSTRACT: A new genus, *Gibsmithia*, is described and tentatively placed in the Dumontiaceae of the red algal order Cryptonemiales. Its diagnostic features are: possession of auxiliary cells in specialized filaments separate from those bearing the carpogonia; the known sexual structures occurring in sori at the tips of soft, gelatinous branches which arise from perennial round stems so as to form a hemispherical head; cruciate tetraspores borne on filaments protruding from the surface of the branches and these same branch filaments often bearing terminal seiospores. The type species of the genus is *G. hawaiiensis*, known only from the island of Oahu in the Hawaiian Islands.

THE ALGA described here was first collected by Dr. J. T. Conover in 1943, and from 1951 on has been found by eight other individuals collecting in Hawaii. It seems to comprise a new genus of the Cryptonemiales in the Rhodophyta, and we take pleasure in naming it in honor of the late Prof. G. M. Smith, of Stanford University, whose publications and teachings have probably done more to facilitate work with the algae in America than has the work of any other phycologist.

Gibsmithia hawaiiensis genus et species nova

Figs. 1-17

DESCRIPTIO TYPI: Thalli ramis gelatinosis fasciculatis, e stipite erecto fere cartilagineo lignoso egredientibus, formam hemisphaericam simulantes. Frondes e filamentis uniseriatis, sicut in genere *Callithamnion*, compositae. Filamenta interdum pilis uniseriatis, multicellularibus e superficie gelatinosa ramorum exstantibus terminata. Tetrasporangia cruciformiter divisa, subsphaerica, in pilis supra descriptis uni-

lateraliter in cymulis fortasse velut in genere *Spermothamnion* producta. Cystocarpia modo *Cryptonemialium* simili crescentia.

The holotype (Fig. 1) was found drifting in the water at Waikiki, Honolulu, Oahu, Hawaii (21° 161 min N, 157° 49.5 min W), on January 12, 1960; 19263.³ It is cystocarpic. The type material, consisting of a liquid-preserved isotype specimen and a dried holotype herbarium specimen, is being deposited in the Bernice P. Bishop Museum in Honolulu, Hawaii. Tetrasporic material has been collected from the vertical surface of a dredge-cut in the reef at Waikiki, first on January 5, 1961, by Dr. D. W. Strasburg. This specimen (8525) is also being deposited in the Bishop Museum herbarium. Other collections are listed below.

DESCRIPTION OF GENUS AND SPECIES: Thalli (Figs. 1, 2), as generally collected, consisting of 'woody' stems and a number of soft, but not slippery, gelatinous ultimate branches. Forming bright-pink, hemispherical tufts often 8 cm high, the stems are up to 3 mm in diameter, blackish when dried, and they bear rings believed to be indicative of successive crops of the ultimate branches. The stems are cylindrical or, when large, compressed toward the apex and sometimes branched once or twice. When the stems are fresh they are colored approximately Eugenia Red or darker to Acajou Red

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³ Such 4- and 5-digit numbers are the collection or herbarium numbers of the author.

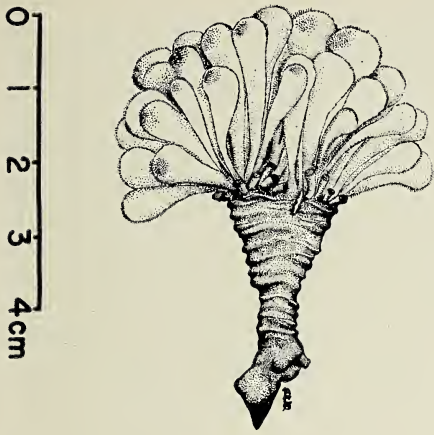


FIG. 1

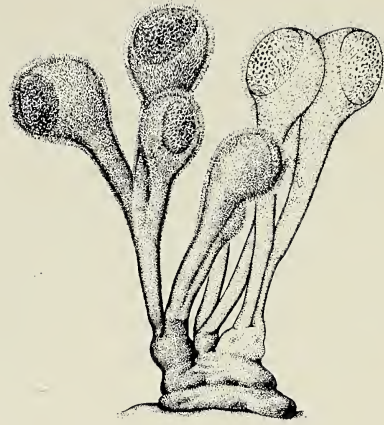


FIG. 2

FIGS. 1-2. Gross aspects of *Gibsmithia hawaiiensis* (type specimen 19263). 1, Whole thallus illustrating the rounded stem with growth rings. 2, A few of the soft gelatinous branches enlarged to show asymmetrical placement of the sexual sori and the superficial filaments which, in tetrasporic thalli, would bear the tetraspores and seiospores. Below is shown some of the stem material of very different, almost woody, nature and the origins and rebranching of the ultimate branches of the thallus.

(Ridgway, 1913). The soft, gelatinous, ultimate branches are lighter red in the same series or their bases are lighter and their apical portions darker. The branches are often up to 4 cm long, and they gradually enlarge apically until they are club-shaped and up to 1 cm in diameter near their tips. These ultimate branches rarely arise singly from the parent stem; more often (Fig. 2) they arise from a disk that is a flattened expanse of the same gelatinous nature and which divides somewhat dichotomously into the branches.

The gelatinous branches are made up of calithamnioid filaments (Fig. 3). The exact nature of the central axis of the thallus has not been determined, but the alga is believed to be multi-axial in structure. The major axes in the medulla bear, most often, opposite branches which seem to arise near the apical cell. Toward the exterior the branching of the filaments is pseudodichotomous, and the surface of a gelatinous branch is generally covered densely, especially toward the tip, with free tufts of such filaments.

Branches of the axial filaments in the medulla

often give rise to recurrent branches (*A* in Figs. 3-5) or rhizoids, which anastomose with a particular cell of another branch (Fig. 3), the supporting cell of the branch (Fig. 4), or with the next cell below in the same branch (Fig. 5). Pit connections appear between all cells concerned in these cases. In content, the cells of such anastomosing branches, like those reported and figured by Feldmann-Mazoyer (1940: 142, 393, fig. 48) in *Pleonosporium borreri*, are not particularly different from the cells of similar nearby filaments.

Reproductive structures of three kinds have been found in the collections studied. These are interpreted as seiospores, as tetrasporangia, or as various stages and structures leading toward carpospore production. The same thallus may produce both tetraspores and seiospores, a situation I have seen in *Seiospora*, and which is reported (Feldmann-Mazoyer, 1940) in *Dobrniella*. The evidences of sexuality have been seen positively in only the type and two other collections. Unfortunately the critical stages involving the primary and secondary connecting filaments between the carpogonia

and auxiliary cells have not been found. Thus, though for the present *Gibsmithia* seems certainly to be a member of the Dumontiaceae as this family is circumscribed by Kylin (1956), the description of the sexual reproduction and discussion of the systematic disposition within the family are of necessity brief.

The seiros spores are borne in unbranched chains at the tips of the exterior filaments in the asexual material. At some place along a branch bearing seiros spores (*B* in Fig. 5) the chromatophore and central vacuole disappear rather abruptly and the cytoplasm (after killing in Karpetchenko's seawater fluid) is then more densely granular and with a refractory body becoming conspicuous as the cells age. The spores, which are about $9\ \mu$ in diameter, appear to become more spherical with maturity, as in *Seiospora*. Their ultimate fate is unknown, but they are broken off easily in preserved material and presumably in nature.

The subspherical tetrasporangia appear on the more basal portions of scattered external filaments similar to those bearing the seiros spores. They are, for the most part, in acropetalous series (Fig. 6) on the adaxial side of the filaments on which they are produced. In a few cases immature tetrasporangia were seen below an otherwise acropetalous series. In some instances what appeared to be chromosome groups undergoing meiosis were distinguished within immature tetrasporangia. The tetrasporangia are apically dehiscent, as in *Antithamnion*, and at least the terminal sporangia were pedicellate. The first division of the cytoplasm in the tetrasporangium (Fig. 7) is near the equatorial plane. Usually the tetraspore pairs are at right angles to each other, i. e., decussately cruciate (Figs. 8, 9); only rarely is a somewhat tetrahedral (Fig. 10) or other (Fig. 11) arrangement seen. The tetraspore groups in the collection 12343 are often as long as 25 or $30\ \mu$ in their major dimension.

The maturing cystocarps, when stained, appear as dots in raised asymmetrically placed welts (Figs. 1, 2) near the tips of the branches. The largest thalli collected, 10386, were believed to be sterile until smears made of the branch tips were examined. When this was done what are accepted as carpogonial branches

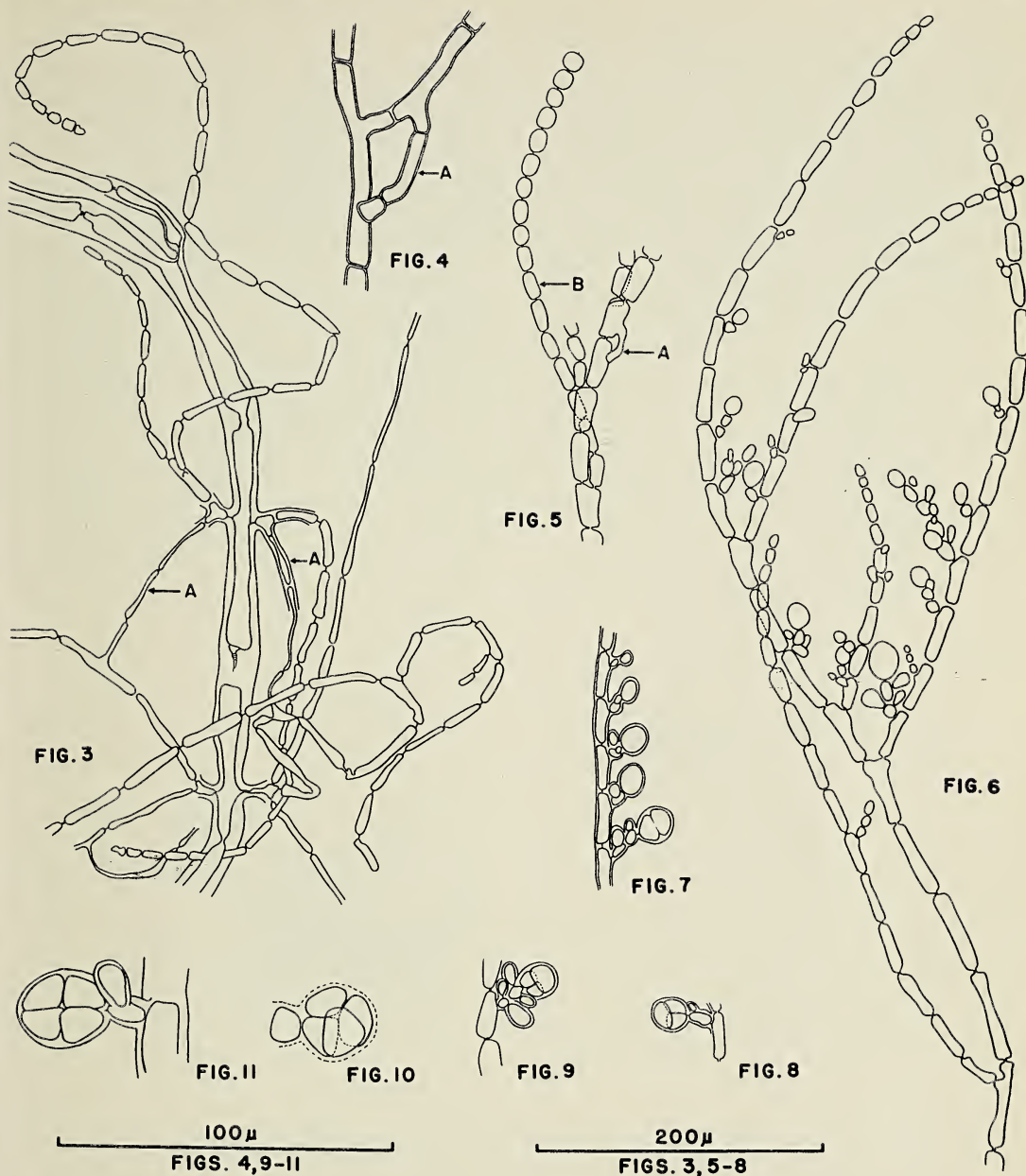
(Figs. 12–14) bearing nonfertilized carpogonia were found.

The carpogonial branch of *Gibsmithia* is the terminal portion of a modified member of the two lateral branch systems arising (Fig. 13) from a cell in a medullary filament. Upon occasion both lateral branch systems bear carpogonia; less frequently only one of the members is carpogonial, and the other is vegetative but reduced in its development. Only monocarpogonial branch systems have been seen. Branching from the cells below the special cells of the carpogonial branch is variable. In some cases there are no such branches (Fig. 12), and in others (e. g., Figs. 13, 14) up to three branches of one to six small cells each occur. The cells of these branches, except for size, are of the same appearance as the homologous cells in vegetative branches nearby.

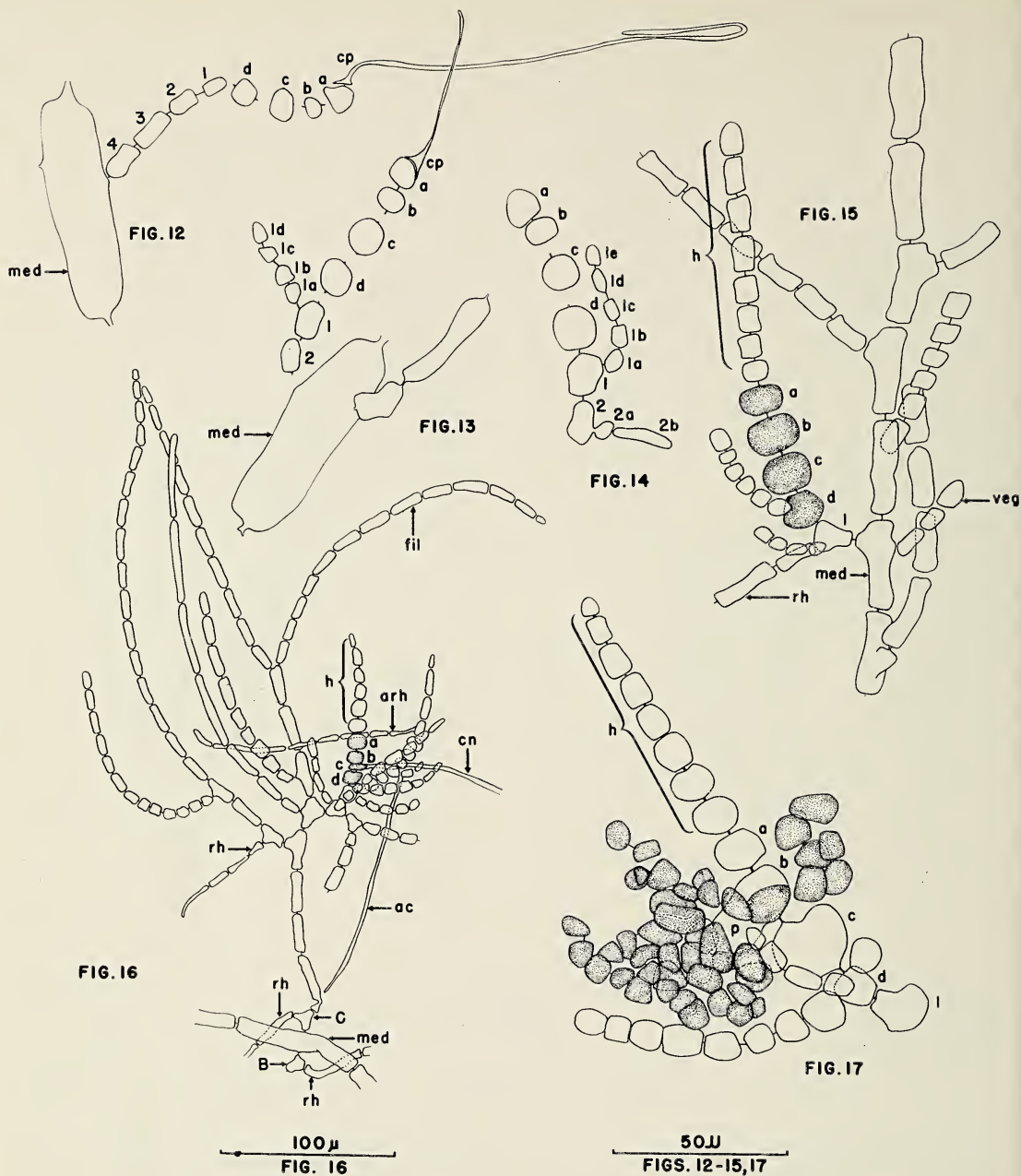
The carpogonial branch itself is consistently composed of five cells (*cp*, *a*, *b*, *c*, and *d* in Figs. 12–14), though the terminal carpogonium is (Fig. 14) not always present. The antepenultimate cell (*b* in Figs. 12, 13) is smaller than the other hypogynous cells. Its contents are often of different appearance and it is flattened, so that its axial length is noticeably less than its diameter. The other three hypogynous cells are more spherical, similar in content, and the largest one (*c* in Figs. 12, 13) is usually about 9 to $13\ \mu$ in diameter. The remaining two (*a*, *d* in Figs. 12, 13) are usually similar in size.

The carpogonium is borne on the first⁴ hypogynous cell excentrically, often by a displacement from the axis of the carpogonial branch of about 45 degrees. The carpogonium (*cp* in Figs. 12, 13) is usually relatively small and does not stain strongly in aniline-blue, in contrast to the other cells of the carpogonial branch.

In the material available, stages were not found which would enable a satisfactorily complete description of sexual reproduction. However, my impression is that the heavily aniline-blue stained condition of almost all carpogonial branches seen is a result of development beyond the fertilizable point. Most such branches consist of either only the cells *a* through *d* (Fig. 14) or have in addition what are interpreted as remnants of a carpogonium. Such carpogonial branches are relatively straight and not



FIGS. 3-11. Vegetative and asexual reproductive microscopic structural details of *Gibsmithia hawaiiensis* (collection No. 12343). 3, An axial filament from the medullary region of a gelatinous branch of the thallus showing the opposite ramification of the medullary filaments and, A, characteristic reconnecting rhizoidal branches. 4, A more simple reconnecting rhizoidal branch, A, from one of the subdichotomous cortical filaments. 5, A seiospore-bearing ultimate branchlet on a subdichotomous cortical filament with, A, a very simple reconnecting filament or rhizoid. Such lateral nonrebranched filaments, B, with a terminal series of seiospores were found arising from almost every second cell in the vegetative axis of this part of the filament system. The origins of but three such seiosporic branches are shown here. 6, A tetrasporangium-bearing cortical filament system. Divisions within the tetrasporangia are not shown and no attempt was made to represent all pit connections. 7-11, Tetrasporangia in various stages of maturity. The arrangement of spores is always at first cruciate but, as indicated by Figure 10, in age they may not be in a strictly cruciate arrangement.



FIGS. 12-17. Microscopic sexual reproductive features of *Gibsmithia hawaiiensis*. The specialized cells, *a-d*, are similar in nature whether in a carpogonial or auxiliary-cell branch. On the latter, the piliform extension, *b*, shows as a multicellular hair, the cells of which are in staining reaction and appearance, rather like vegetative cells of similar size and relative terminal position elsewhere. 12-14, Carpogonial branches with or without nonfertilized carpogonia, *cp*. The hypogynous cells *a-d* were always densely granular and their contents took up aniline-blue from aqueous solution much more than did the other nearby cells. Cell *b* was usually smaller and the contents were usually different from the rest. Cell *c* was almost always the largest. The numbered cells, 1, 2, 3, etc., represent cells that looked like the strictly vegetative cells of similar size and position nearby and connected the carpogonial branch to a medullary cell, *med*. The cytologically similar cells of the sterile branchlets are indicated as *1a*, *1b*, *1c*, etc. (Collection No. 10386.) 15, A nonfertilized auxiliary-cell branch arising from one of two opposite branch systems of the same medullary cell, *med*, the one vegetative branch system, *veg*, being of only three cells, the other more extensive and bearing an auxiliary-cell branch.

strongly curved apically, as is usual in the Dumontiaceae. In a very few cases carpogonium-bearing branches that are more curved are found with hypogynous cells that are less highly differentiated in staining quality and in form. In these cases the hypogynous and carpogonial cells are more nearly similar in staining quality and are smaller; such (Fig. 12) are judged to be more nearly normal.

Primary connecting filaments⁴ were not seen, and no clues as to the origin of the abundant, presumed secondary, connecting filaments that connect to the auxiliary cells were found. In a very few cases the carpogonium as well as the cell beneath it were seen to have some indication of protuberances extending toward one another or toward the smallest of the hypogynous cells. This could have been the effect of smearing the material for microscope examination.

The auxiliary-cell branches (Fig. 15) develop

⁴The author is attempting to apply terms to the post-fertilization morphological phenomena in such a way that they are consistent with general biological usage, and so that the frequent special cases and variations from the normal do not require a special nomenclature. Thus, the term "zygote" is used for the post-fertilization carpogonium and its contents, and "primary connecting filament" for the connection between the zygote and the auxiliary cell without distinguishing whether a "carpogonial" or "generative" auxiliary cell is concerned. "Secondary connecting filament" is used to refer to any connecting filament ("ooblast" of the older nomenclature) arising from an auxiliary cell. Similarly, the term "hypogynous" is used for any of the specialized cells of the carpogonial branch other than the carpogonium itself; these are referred to as *a*, *b*, *c*, etc., or the "first," "second," etc., proceeding away from the carpogonium.

farther from the apex than the carpogonial branches. It may be that initiation, or at least maturation, of an auxiliary-cell branch system is dependent upon fertilization, for in 10386, where many nonfertilized carpogonial branches were found, especially of the forms illustrated in Figures 13 and 14, branches bearing mature auxiliary cells were not observed. They are usually in the same positions as carpogonial branches, or, at times, appear to have developed (Fig. 16) after the lateral branch system had grown further.

While the complement of cells in the auxiliary-cell branches is similar in number, form, arrangement, and appearance to the hypogynous cells in a carpogonial branch, there are two major differences: in place of the carpogonium there is a reduced terminal branch or row of vegetative cells, and there are more sterile filaments developed laterally from and near the base. The auxiliary cell itself is an intercalary cell, and, contrary to the condition illustrated in Figures 15 and 16, is usually the cell there labeled as *b*.

The presumed secondary, connecting filaments (*cn* in Fig. 16) were seen fused with the auxiliary cells (*c* in Fig. 16). The tissue of the weltlike sori (Fig. 2) in which cystocarps develop is the toughest of all parts of the branch surface and this toughness seems to be related to the great abundance of sterile branches appearing in the fertile system, as well as to numerous, presumed secondary, connecting filaments. In addition, multicellular rhizoidal branches from the bases of the branch filaments (*rh* in Figs. 15, 16, and possibly *A*

This particular auxiliary-cell branch would seem to be peculiar, for usually one of the two cells labeled *b* and *c* is about half the size of the cells labeled *a* and *d*, which are similar in size. The other cell, *c* or *b*, is usually distinctly the largest of the four. A rhizoidal branch, *rh*, arises from the single vegetative cell, *l*, connecting this auxiliary-cell branch system to the medullary system. (Collection No. 19263.) 16, A lateral branch system arising as one of a pair, *B* and *C*, from a single medullary cell, *med*, and producing vegetative filaments, *fil*, and rhizoidal filaments, *rh*, in a normal manner, and showing (at *c*) a fertilized auxiliary cell. Two other types of filaments are illustrated here: what may be labeled as an accessory rhizoid, *arb*, of multicellular nature arising near a fertilized auxiliary cell and, *ac*, an accessory connecting filament. The auxiliary cell, *c*, is shown with a connecting filament, *cn*, associated. The actual relationships of cells, *c*, *cn*, and *ac*, to one another were not entirely clear at the highest magnifications. (Collection No. 19263.) 17, A young gonimoblast showing the apparent carposporogenic cells heavily stippled. Cell *l*, seemed to correspond to cells *B* and *C* in Figure 16. Cell *d* bore three vegetative branches in addition to the auxiliary-cell branch. No connecting filament could be distinguished. Seemingly, the auxiliary cell, *b*, had produced the gonimoblast to the left at the tip of the expansion, *p*, from but one gonimoblast initial. The six cells to the right seemed unattached and were interpreted as having been broken free from the mass at the left. (Collection No. 19263.)

in Fig. 3) are abundant, and undoubtedly contribute to the strength of the otherwise weak, gelatinous, branch substance.

The surface of the auxiliary cell (*b* in Fig. 17), beneath the connecting filament, apparently develops a protrusion that moves the connecting filament away from the auxiliary-cell branch axis. From this protuberance of the auxiliary cell (*p* in Fig. 17) gonimoblast initials arise. While the gonimoblast, upon smearing, reveals its fundamentally filamentous nature (Fig. 17), in the undisturbed condition it is a dense almost spherical mass. Older gonimoblasts have one (or a few) very large cells at the center: all the other cells appear to be uniform, as though all could become carposporangia in time.

MATERIALS EXAMINED (all from the island of Oahu, Hawaii; the collection numbers are the author's, except the first): *J. T. Conover*, 200 BERKELEY,⁵ tetrasporic, found about 550 ft along a line extending about 113° from the old marine laboratory at Waikiki on underside of a coral head about halfway out on the reef at a depth of 1.2 m, VIII-43; *D. W. Strasburg*, 8525 (BISHOP) tetrasporic and seiosporic, University of Hawaii old beach laboratory, Waikiki, Honolulu (21° 16.2' N, 157° 49.6' W), I-51; *M. Doty*, 8562 (STANFORD), another branch of the same thallus as 8525, but collected 25 days later; *George Ikeda*, 10385 (AUSTRALIA) tetrasporic, Lae o Kaoio, Kua-Loa, Kaaawa, one of two clumps seen in 5 ft of water, II-52; *George Ikeda*, 10386 (STANFORD, BERKELEY) carpogonial, in 4-5 ft of water on limestone bottom (same area as Ikeda collection of II-52, above), V-52; *Jack Randall*, 17020 (BERKELEY) seiosporic, drifting freely below the surface off Oahu, Hawaii, VI-52;

M. Doty, 12343 (STANFORD) tetrasporic, floating freely at the surface just north of the mouth of Koloa stream south of Laie, I-54; *M. Doty*, 12286 (HOKKAIDO) first of a series of collections from the same tetrasporic thallus growing about 7 ft below the surface along the inshore edge of the swimming channel in front of the new University of Hawaii beach laboratory at Waikiki, Honolulu, XII-52; *M. Doty*, 12652 and 12647 (PARIS) tetrasporic, both same thallus as 12286, about X-54; 17019 (BISHOP) sterile, same thallus as 12286, III-55; *Jan Newhouse* and *Malvern Gilmartin*, 12671 (VANCOUVER) tetrasporic, beyond the reef, Waikiki, Honolulu, XI-54; HOLOTYPE, *M. Doty* and *B. C. Stone*, TYPE 19263 (BISHOP) cystocarpic, drifting at the surface, Waikiki, Honolulu, (near 21° 16' N, 157° 49.5' W), I-60; *Elvin Fong*, 19478 (STANFORD) cystocarpic and tetrasporic, on a 3 by 4 ft rock in 15 to 20 ft of water 150 yd off Haleiwa Army Beach near the channel at Haleiwa, VI-55.

This is one of the less common algae occurring along the shores of Oahu in Hawaii. It has been found adrift in a few cases, but for the most part it is found growing 1 to 2 m below low tide on reef flats. The hemispherical pale thalli were often found growing in a concavity or on a vertical surface. One individual thallus, near the University's aquarium and beach laboratory at Waikiki in Honolulu, was watched and pieces were harvested from it at irregular intervals for about 3 yr. The deepest collection was that made by Jan Newhouse and Dr. Malvern Gilmartin from the base of a coral patch on rock bottom in 7 m of water about 1000 m beyond the reef opposite the Natatorium at Waikiki.

The stem, the perennial nature of the thallus and some of the reproductory features of *Gibsmithia* show some resemblance to the much recopied small portion of Gmelin's specimen (1768: pl. 5, fig. 2) of *Constantinea*⁶ (e. g., Kylin, 1956: fig. 102).

It is to be noted that at least three collections of *Gibsmithia*, including the type, were of free-floating branches. It would appear that the

⁵ Names appearing in this position refer to the following repositories of the particular material: BISHOP, B. P. Bishop Museum, Honolulu, Hawaii; STANFORD, Hopkins Marine Station of Stanford University, Pacific Grove, Calif.; BERKELEY, Herbarium of the University of California, Berkeley, Calif.; PARIS, Laboratoire de Cryptogamie du Museum National d'Histoire Naturelle; AUSTRALIA, Herbarium of the University of Adelaide, Adelaide, S. Australia; HOKKAIDO, Herbarium of the Faculty of Science, Hokkaido University, Sapporo, Japan; VANCOUVER, Herbarium of the University of British Columbia, Vancouver, British Columbia.

⁶ The figure given by Okamura (1912: pl. 77, figs. 1, 2) conveys a rather different conception of this alga—a more correct one it would seem.

branches are deciduous at maturity, as is the disklike peltate blade of *Constantinea simplex*. However, the many quite different features of *Constantinea*, especially as revealed by Masaki (1952), indicate that *Constantinea* could be, at best, but remotely related to *Gibsmithia*.

Some of the anatomical features, the seirospores, and tetrasporangia are reminiscent of the Ceramiaeae. Yet I believe *Gibsmithia* should be placed among the primitive Cryptonemiales for several reasons, most notable of which is the occurrence of the carpogonia and the auxiliary cells in separate but similar special branch systems. In their general morphology and in having a small differentiated cell among the enlarged hypogynous cells, the carpogonial branches of *Gibsmithia* (if, indeed, we have seen normal carpogonial branches) recall both the carpogonial and auxiliary-cell branches of *Dudresnaya crassa*, as I have seen them in material collected by Dr. A. J. Bernatowicz in Bermuda (his number 51-580), and as they are illustrated by Taylor (1950: figs. 5-7, 38) in his splendid account of the reproduction of that species.

The terminal row of sterile cells distinguishes an auxiliary-cell filament from a carpogonial branch with its terminal trichogyne. While the terminal row of sterile cells is distinct from the terminal part of a normal vegetative branch, it is less specialized than the "hair" to be seen in *Dudresnaya crassa* and which Taylor (1950: figs. 36, 37) refers to as a "piliform extension." In other features *Gibsmithia* also recalls such a genus as *Dudresnaya* rather than any of the polycarpogonial forms discussed by Norris (1957), which are far more complex. It is like *Thuretellopsis* (Kylin, 1925: 14) in that the carpogonial and auxiliary-cell branches are alike; but in *Gibsmithia* they are less compact and less specialized. In having a terminal row of sterile cells and in having a larger number of cells, the auxiliary-cell filaments of *Gibsmithia* would seem to be more primitive than those of *Thuretellopsis*.

A point of some systematic interest is the development of low, wartlike sori containing the cystocarps. The tetrasporangia are borne quite differently, being exposed as in the Ceramiaeae. These two features seem to set this genus apart from most of the other genera now

placed in the Dumontiaceae. The possession of cruciately divided tetrasporangia further distinguishes *Gibsmithia* from the type genus of the Dumontiaceae and likens it to families such as the Squamariaceae of the Cryptonemiales which have cruciate tetrasporangia and the reproductive structures in nemathecia. Until the simpler cryptonemiaceous families are better known, it seems best to place *Gibsmithia* tentatively among the Dumontiaceae.

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Revision of the Genus *Pandanus* Stickman, Part 16 Species Discovered in Thailand and Vietnam

HAROLD ST. JOHN¹

THE FOLLOWING NEW species are all but one based upon specimens collected by others and preserved in Bangkok, either in the herbarium of the Department of Agriculture at Kasetsart University or in the herbarium of the Royal Forestry Department.

SECTION *Acrostigma*

Pandanus biplicatus sp. nov. (sect. *Acrostigma*)

Fig. 192

DIAGNOSIS HOLOTYPE: Licet acaulescens, foliis 1.01 m longis 3.6 cm latis parte $\frac{1}{3}$ basali subcoriacea parte ultima crassiter chartacea supra viridibus infra pallidis et licet glaucis 1-sulcatis acute 2-plicatis in sectione mediali M-formatis et cum 41 nervis parallelis secundariis in quoque dimidio, nervis tertilis in parte $\frac{2}{3}$ ultima conspicuis et reticulis anguste oblongis formantibus, laminis ligulatis subiter in apice trigono subulato 3 cm longo 1–2 mm lato diminuentibus basi amplexicauli et inermi sed ex 14–15 cm marginibus cum aculeis 1.5–2 mm longis 2–8 mm separatis subulato-serratis complanatis luteis, midnervo infra ex 20 cm cum aculeis 2–3.5 mm longis 8–15 mm separatis subulatis reflexis, in sectione mediali marginibus cum aculeis 1.5–2 mm longis 5–10 mm separatis subulatis proxime adscendentibus, midnervo infra cum aculeis 2.5–3 mm longis 15–22 mm separatis subulatis adscendentibus, in apice subulato marginibus et midnervo infra cum serrulis 0.2–0.3 mm longis 1.5–3 mm separatis, in pagina superiori ad apicem plicis cum serrulis 0.2–0.3 mm longis 1–4 mm separatis, inflorescentia foeminea erecta et recta, pedunculo 22–30 cm longo gracili clavato 9–12 mm diametro in apice folioso bracteato, bracteis herbaceis coloratis sed in sicco

nigro-brunneis infima 19 cm longa 23 mm lata lineari-lanceolata ad basem integra parte $\frac{1}{3}$ ultima proxime subulato-serrata, syncarpio 9.5 cm longo 7.2 cm diametro obovoideo-ellipsoideo cum drupis numerosis, eis 32–34 mm longis 6–7.5 mm latis 4–6 mm crassis anguste oblanceo-fusiformibus 1-carpelatis parte $\frac{1}{3}$ supera libera corpore 24–26 mm longo oblanceoloideo lateribus planis, pileo 13–14 mm longo cartilagineo basi 5–6 mm alta rotundato-pyramidalis 6-angulata, stylo 6–8 mm longo crassiter subulato anguloso divergenti subsinuoso, stigmatibus 3–4 mm longo distali lineari brunneo sulcato papilloso in apice extenso, endocarpio in parte $\frac{1}{3}$ infera obovoideo cartilagineo stramineo in apice truncato lateribus 0.1 mm crassis, semine 8–9 mm longo obovoideo, mesocarpio apicali 7 mm longo cum medulla alba delicata completa, mesocarpio basali 5–6 mm longo fibroso et carnosio.

DIAGNOSIS OF HOLOTYPE: Perhaps acaulescent; leaves about 1.01 m long, 3.6 cm wide, the lower $\frac{1}{3}$ subcoriaceous, the outer $\frac{2}{3}$ thick chartaceous, green above, pale and apparently glaucous below, 1-furrowed above the midrib, sharply 2-pleated, at midsection M-shaped in section and with 41 parallel secondary veins in each half, tertiary cross veins conspicuous in outer $\frac{2}{3}$'s, forming narrow oblong meshes, the blade ligulate, abruptly narrowed to a trigonous subulate apex 3 cm long, 1–2 mm wide, the base amplexicaul and unarmed, but beginning at 14–15 cm the margins with prickles 1.5–2 mm long, 2–8 mm apart, subulate-serrate, flat, yellowish; the midrib below beginning at 20 cm with prickles 2–3.5 mm long, 8–15 mm apart, subulate, reflexed; at midsection the margins with prickles 1.5–2 mm long, 5–10 mm apart, subulate, closely ascending; the midrib below with prickles 2.5–3 mm long, 15–22 mm apart, subulate, ascending; on the subulate apex the margins and midrib below with serrulations 0.2–0.3 mm long, 1.5–3 mm apart; on upper

¹ B. P. Bishop Museum, Honolulu 17, Hawaii, U.S.A. Manuscript received September 28, 1961.

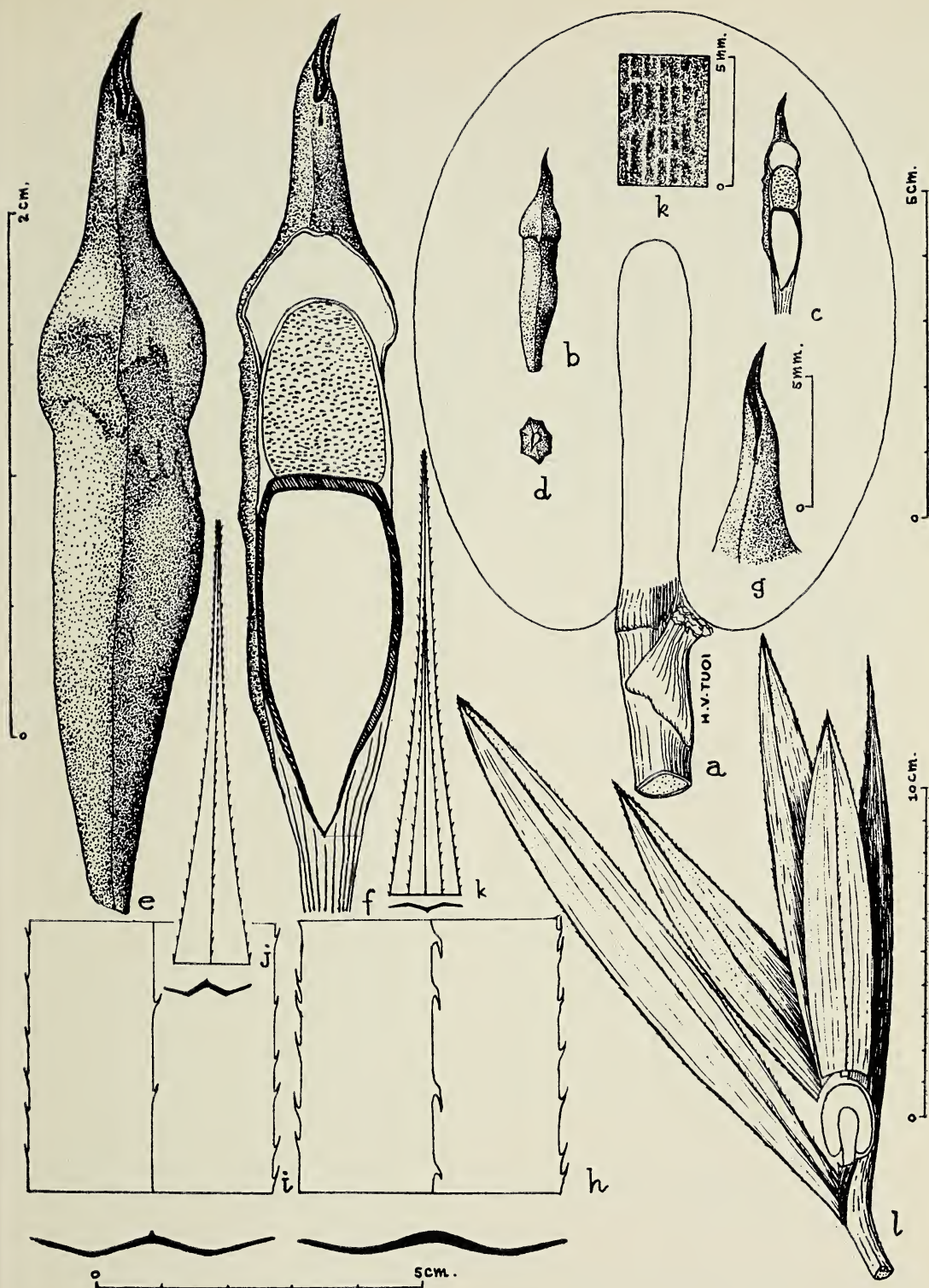


FIG. 192. *Pandanus biplicatus* St. John, from holotype. *a*, Syncarp profile, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, apical view, $\times 1$; *e*, drupe, lateral view, $\times 4$; *f*, drupe, longitudinal median section, $\times 4$; *g*, style and stigma, distal view, $\times 4$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$; *k*, leaf apex, upper side, $\times 1$; *l*, young pistillate inflorescence, lateral view, $\times \frac{1}{2}$.

side towards the apex the pleats with serrulations 0.2–0.3 mm long, 1–4 mm apart; pistillate inflorescence erect, straight; peduncle 22–30 cm long, slender clavate, 9–12 mm in diameter at apex, leafy bracted; floral bracts herbaceous, colored, drying blackish brown, the lowest one 19 cm long, 23 mm wide, linear-lanceolate, entire below, the outer $\frac{1}{3}$ closely subulate-serrate; syncarp 9.5 cm long, 7.2 cm in diameter, obovoid-ellipsoid, with numerous drupes, these 32–34 mm long, 6–7.5 mm wide, 4–6 mm thick, narrowly oblance-fusiform, 1-celled, upper $\frac{1}{3}$ free, the body 24–26 mm long, oblanceoloid, the sides flat; pileus 13–14 mm long, cartilaginous, the base 5–6 mm high, rounded pyramidal, 6-angled, tapering upwards; style 6–8 mm long, stout subulate, angled, divergent, slightly sinuous, but nearly straight; stigma 3–4 mm long, distal, linear, brown, creased, papillose, running to the apex; endocarp in lower $\frac{1}{3}$, obovoid, the apex truncate, cartilaginous, stramineous, the walls 0.1 mm thick; seed 8–9 mm long, obovoid; apical mesocarp 7 mm long, filled with a delicate white pith; basal mesocarp 5–6 mm long, fibrous and fleshy.

HOLOTYPE: Thailand, Lower Siam, Kopah, Jaujau, 9 Dec. 1917, *Md. Haniff & Md. Nur* 2,703 (SING).

DISCUSSION: *P. biplicatus* is a member of the section *Acrostigma*, as is its closest relative, *P. pseudofoetidus* Martelli of Burma, a species which has the syncarp subglobose; drupes 20 mm long, 5 mm wide; endocarp 10 mm long; and the apical mesocarp 4 mm long. *P. biplicatus* has the syncarp obovoid-ellipsoid; drupes 32–34 mm long, 6–7.5 mm wide; endocarp 13 mm long; and the apical mesocarp 7 mm long.

The new epithet is from the Latin, *bi*, twice, *plicatus*, folded, in reference to the two longitudinal pleats of the leaves.

Pandanus monotheca Martelli, Soc. Bot. Ital., Bul. 303, 1904; Webbia 4(2): pl. 41, fig. 18–20, 1914.

THAILAND: Bāchaw, Pattani, evergreen forest, 600 m. alt., July 14, 1923, *A. F. G. Kerr* 7,191 (BK). This species, originally described from Malaya, is here recorded for the first time for Thailand.

Pandanus Toei sp. nov. (sect. *Acrostigma*)

Figs. 193, 194

NOM. VERN.: "toei."

DIAGNOSIS HOLOTYPI: Acaulescens, foliis 1.3 m longis in media 20 mm latis proxima basem 15–18 mm latis supra midervum sulcatis 2-plicatis chartaceis supra viridibus infra pallidioribus ligulatis in apice 9 cm longo 0.3–0.8 mm lato subulato trigono in sectione mediali cum 26–29 nervis secundariis parallelis in quoque latere, nervis tertilis non evidentis basi amplexicauli et inermi sed ex 4.5–6.5 cm marginibus cum aculeis 1.3–2 mm longis 3–7 mm separatis subulatis adscendentibus luteis, midnervo infra ex 6–8.5 cm cum aculeis 1.5–2.5 mm longis 6–15 mm separatis crassiter subulatis arcuatis reflexis, in sectione mediali marginibus cum serrulis 0.2–0.6 mm longis 3–7 mm separatis, midnervo infra cum aculeis 2 mm longis remotis subulatis arcuatis reflexis vel adscendentibus, in apice subulato marginibus et midnervo infra cum serrulis 0.2 mm longis 0.5–2 mm separatis, inflorescentia foeminea terminali erecta cum syncarpio unico, pedunculo 15 cm longo clavato trigono in apice 5 mm diametro in dimidia ultima cum bracteis foliosis paucis eis superis 40–50 cm longis 15–18 mm latis, syncarpio 3.5 cm diametro globoso viridi cum circa 160 drupis, eis 15–18 mm longis 4–5 mm latis 3–4 mm crassis subfusiformibus parte $\frac{2}{3}$ supera libera corpore oblanceo-ellipsoideo obtuso 10–12 mm longo, pileo 9–11 mm longo basi 2–3 mm alto oblato-pyramidalis-hemispherico laevi 5–7-anguloso angulis in stylo continuis, stylo 5–7 mm longo valido 5–7-anguloso subulato proxime arcuato parte exteriori osseosa lucida lutea, stigmatate 2.5–3 mm longo distali sublineari sulcato brunneo papilloso paene ad apicem extento, endocarpio in tertia infera cartilagineo luteo muris 0.1 mm crassis intra lucidis, semine 6–7 mm longo 2–2.5 mm diametro oblanceoloideo truncato, mesocarpio apicali 2 mm longo hemispherico vel oblato-hemispherico et cum membranis medullosis albis, mesocarpio basali fibroso et carnosio.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Acaulescent, or decumbent with the stem 20 cm tall, 12–22 mm in diameter, brown, smooth; leaves 0.96–1.3 m long, 20 mm wide near the middle, 15–18 mm wide near the base, 1-fur-

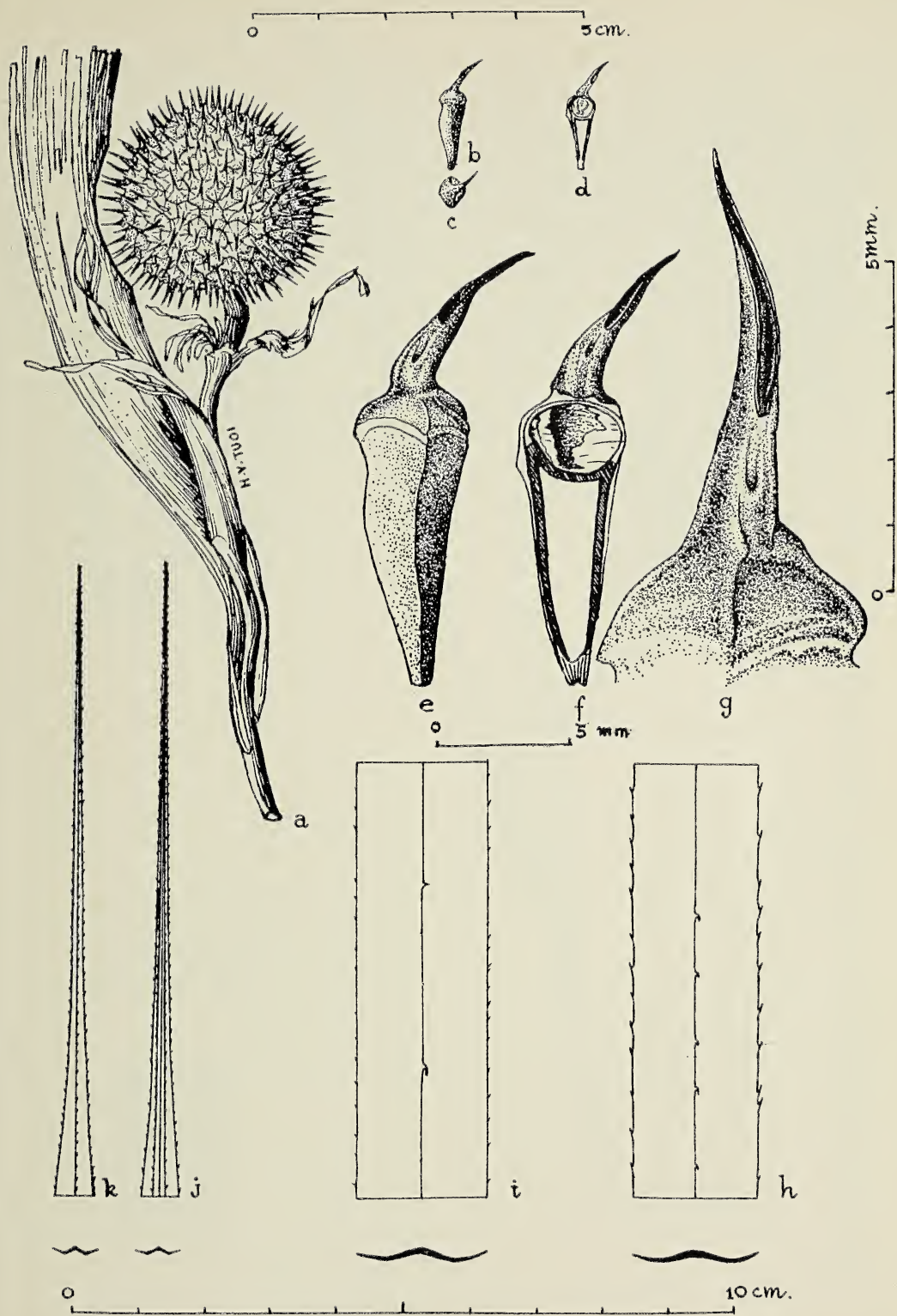


FIG. 193. *Pandanus Toei* St. John, from holotype. *a*, Peduncle and syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, apical view, $\times 1$; *d*, drupe, longitudinal median section, $\times 1$; *e*, drupe, lateral view, $\times 4$; *f*, drupe, longitudinal median section, $\times 4$; *g*, style and stigma, distal view, $\times 10$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, upper side, $\times 1$; *k*, leaf apex, lower side, $\times 1$.



FIG. 194. *Pandanus Toeï* St. John, from Smitinand 1,391. a, Staminate inflorescence, $\times 1$; b, axis and stamens, $\times 10$; c, leaf base, lower side, $\times 1$; d, leaf middle, lower side, $\times 1$; e, leaf apex, upper side, $\times 1$; f, leaf apex, lower side, $\times 1$; g, secondary longitudinal veins and tertiary cross veins, at midsection, lower side, $\times 4$.

rowed over the midrib, 2-pleated, chartaceous, green above, paler green below, ligulate, tapering to a 9 cm subulate, trigonous apex 0.3–0.8 mm wide, at midsection with 26–29 secondary parallel veins in each half, the base unarmed, but beginning at 4.5–6.5 cm the margins with prickles 1.3–2 mm long, 3–7 mm apart, subulate, ascending, yellowish; the midrib below beginning 6–8.5 cm up with prickles 1.5–2.5 mm long, 6–15 mm apart, stout subulate, fully reflexed arcuate; at midsection the margins with serrulations 0.2–0.6 mm long, 3–7 mm apart, the midrib below with remote prickles 2 mm long, subulate, arcuate, reflexed or ascending; on the subulate tip the margins and midrib below with serrulations 0.2 mm long, 0.5–2 mm apart; pistillate inflorescence terminal, erect, with 1 syncarp or rarely with a small secondary one; peduncle 15 cm long, clavate, trigonous, 5 mm in diameter at apex, with a few leafy bracts on upper half, the upper bracts 40–50 cm long, 15–18 mm wide; syncarp 2.5–4.5 cm in diameter, globose to ellipsoid, green, bearing about 160 drupes, these 15–18 mm long, 4–5 mm wide, 3–4 mm thick, subfusiform, upper $\frac{2}{3}$ free, the body oblance-ellipsoid, obtuse, 10–12 mm long; pileus 9–11 mm long, the base 2–3 mm high, oblate pyramidal-hemispheric, smooth, 5–7-angled, the angles continuing well up the style; style 5–7 mm long, stout, 5–7-angled, subulate, proximally arcuate, the outer part bony, shining, yellowish; stigma 2.5–3 mm long, distal, sublinear, creased, brown, papillose, running almost to the apex; endocarp in lower $\frac{1}{3}$, cartilaginous, yellowish, the walls 0.1 mm thick, the inside shining; seed 6–7 mm long, 2–2.5 mm in diameter, oblanceoloid, truncate; apical mesocarp 2 mm long, hemispheric or depressedly so, containing white, medullary membranes; basal mesocarp fibrous and fleshy.

STAMINATE PLANTS: Prostrate, stems 7–11 mm in diameter, very short; leaves 80–90 cm long, 18 mm wide at the middle and base, the subulate apex 3–4 cm long, at midsection with 24–27 parallel secondary veins in each half; staminate inflorescence almost erect, 18 cm long, fragrant; peduncle 7 cm long; flowering part 11 cm long, with conspicuous yellow bracts, the lowest one 9.5 cm long, 16 mm wide, linear

lanceolate, chartaceous, serrulate only on the short subulate tip; median bract 6 cm long, 14 mm wide, lanceolate, the margins of the outer half and the midrib below near the tip with pale, fragile serrulations 0.1 mm long; spikes about 7 and 1.5–2 cm long, 8–15 mm in diameter, dense; stamens numerous, attached singly, directly to the axis; filaments 0.1–0.2 mm long; anthers 6–7 mm long, linear, bearing at the apex a projection of the connective 0.2–0.3 mm long, sometimes subulate but more commonly flat, lanceolate, obtuse.

HOLOTYPE: Thailand, Peninsular, Krabi, 83 km. from Huay Yawt, very common in moist localities by roadside, 100 m. alt., 28 Jan. 1958, *Tem Smitinand* 4,143 (BKF).

SPECIMENS EXAMINED: Thailand, Trat, Koh Chang, shrub in evergreen forest by stream, 40 m. alt., 19 Feb. 1954, (BKF); erect shrub 40 cm. tall, common in swampy ground in evergreen forest, 1 June 1952, *Bunnak* (*Sang Kachand*) 333 (BKF); Trat, Huayraent, *Tem Smitinand* 1,392 (BKF); Peninsula, Trang, Kantang, Khuan nang hong, less than 100 m. alt., common in evergreen jungle, 26 Aug. 1955, *Tem Smitinand* 3,012 (BKF); S. E. Part, Trat, Kaw Kut, Ao Salat, common in evergreen forests, 5 m. alt., 5 April 1959, *Tem Smitinand* 5,702, staminate, (BKF); S. E. Part, Trat, Huang Raeng, Dong Tapit, prostrate, common in swamp by path in evergreen jungle, under 50 m. alt., 21 June 1952, *Tem Smitinand* 1,391, staminate, (BKF no. 7,276); Kasvon, Nov. 1896, *C. Curtis* 3,247 (SING).

MALAYA: Penang, near Tanjong Toking, July 1889, *C. Curtis* 1,821 (SING); Perak, Lahat, Ipoh, Oct. 1904, *H. N. Ridley*, (SING), one of the original paratypes of *P. perakensis* Ridl.

DISCUSSION: *P. Toei* is a member of the section *Acrostigma*, as is its closest relative, *P. Kinnianus* Martelli of Malaya, a species which has the drupes 11–13 mm long; style 5 mm long; pileus rounded; and the leaves 40–50 cm long, 14 mm wide. *P. Toei* has the drupes 15–18 mm long; style 5–7 mm long; pileus prominently angled; and the leaves 96–130 cm long, 20 mm wide.

The new epithet is the vernacular name of the plant in its native region in Thailand.



FIG. 195. *Pandanus calcis* St. John, *a-e, b-j*, from holotype; *f-g* from Kerr 13,358. *a*, Syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, apical view, $\times 1$; *e*, drupe, median transverse section through horizontal plate, $\times 4$; *f*, drupe apex and stigma, proximal view, $\times 4$; *g*, drupe apex and stigma, lateral view, $\times 4$; *h*, leaf base, lower side, $\times 1$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$.

SECTION *Microstigma**Pandanus calcis* sp. nov. (sect. *Microstigma*)

Fig. 195

NOM. VERN.: "lang kai."

DIAGNOSIS HOLOTYPI: Truncus 3 m altus ramosus eo ramisque cum "spinis brevibus armatis," foliis 75 cm longis 2–2.5 cm latis tenuibus sed subcoriaceis infra subpallidioribus supra sulcatis marginibus subrevolutis in sectione mediali cum 32 nervis secundariis in quoque latere ligulatis sed sensim in apice subulato longe diminuentibus eo 10 cm ex apice 4 mm lato basi exarmatis sed ex 4 cm marginibus cum serris fortibus arcuatis subulatis 1–2 mm longis 5–15 mm distantibus toto obscure brunneis, midnervo infra inermi, in sectione medialis marginibus cum dentibus 0.2–0.5 mm longis 6–8 mm distantibus subulatis toto adpressis adscendentibus brunneis, midnervo infra cum dentibus simulantibus 3–8 mm distantibus, circa apicem marginibus cum serris 0.2–0.3 mm longis 4–9 mm distantibus brunneis, midnervo infra cum serulis simulantibus 13–15 mm distantibus, pedunculo 7 cm longo 7 mm diametro trigono folioso, syncarpio subgloboso 6 cm diametro terminali solitario erecto cum 26 drupis eis 3.2–3.4 cm longis 1.7–2 cm latis 1.7–1.8 cm crassis (sed in gemino 2.6 cm latis) ellipsoideis in sicco brunneis obovoideis sed basi cuneata lateribus laevibus sublucidis 5-angulatis angulis subrotundatis parte ½ supera libera, apice rotundato sed biangulatis, stigmatibus 3 mm longo excentrico obdeltoideo cordato sulcato obscure brunneo papilloso valde oblique et proximo, endocarpio supramediis osseoso obscure brunneo 12–13 mm longo lateribus 2 mm crassis, semine 6 mm longo adamantino sed trilobato, mesocarpio apicali plerumque medullosa sicco, mesocarpio basali fibroso et medullosa.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Trunk 3–5 m tall, branching, it and the branches "armed with short spines"; leaves 75–84 cm long, 2–2.7 cm wide, rather thin but subcoriaceous, slightly paler beneath, above with a central furrow and the margins gently down-rolled, at midsection with 32 secondary veins in each half, ligulate but gradually long tapering to the subulate apex which 10 cm down is 2–4 mm wide, the base unarmed for 4 cm then the mar-

gins with heavy arcuate subulate serrations 1–2 mm long, 5–15 mm apart, wholly dark brown, the nearby midrib below unarmed; at the midsection the margins with the teeth 0.2–0.5 mm long, 6–8 mm apart, subulate, fully appressed ascending, brown; the midrib below with similar teeth 3–8 mm apart; near the tip the margins with brown serrations 0.2–0.3 mm long, 4–9 mm apart, the midrib below with similar serrations 13–15 mm apart; peduncle 7 cm long, 7 mm in diameter, 3-angled, leafy bracted; lower bracts 25–33 cm long, 15 mm wide, distended and paler at base; syncarp subglobose 6–7 cm in diameter, terminal, solitary, erect, bearing 20–26 drupes, these 3.2–3.8 cm long, 1.7–2.1 cm wide, 1.7–1.8 cm thick, (but in a twinned one 2.6 cm wide), ellipsoid, when dried brown, obovoid but the base cuneate, the sides smooth, somewhat shiny, 5–6-angled, the angles more rounded than sharp, upper ½ free, the apex rounded, but two lateral angles produced into the sharp ridges curving and leading to the excentric stigma; stigma 2.5–3.5 mm long, obdeltooid cordate or oblong cordate or lance-cordate, creased, dark brown, papillose, sharply oblique and proximal; endocarp suprmedian, bony, dark brown, with two vertical columns near the center, 12–13 mm long, a narrow transverse median plate connecting to the marginal vertical flanges 2 mm thick; seed 6 mm long, diamond-shaped but with 3 ascending lobes; apical mesocarp mostly of dry, membranous pith; basal mesocarp fibrous and pithy.

HOLOTYPE: Thailand (Siam): Kao Tala, Ranawng, on limestone rocks, 200 m. alt., Feb. 3, 1927, *A. F. G. Kerr* 11,796 (BK).

SPECIMENS EXAMINED: Thailand, Kaw Wieng, Chumpawn, limestone rocks, 50 m. alt., Jan. 11, 1927, *A. F. G. Kerr* 11,373, nom. vern. "chan deng," (BK); Ban Kawp Kep, Surat, forming pure growth on top of limestone hill, 100–200 m. alt., Aug. 16, 1927, *Kerr* 13,358 (BK); Sapli, Chumpawn, Sept. 8, 1927, Put, *A. F. G. Kerr* 1,018 (BK); Kantuli, Surat, Sept. 10, 1931, Put, *A. F. G. Kerr* 4,189 (BK).

DISCUSSION: *P. calcis* is a member of the section *Microstigma*, as is its nearest relative, *P. utilissimus* Elmer, of the Philippines, a species which has the syncarp 60 cm long, 20 cm in diameter; drupes 4.5–7 cm long, linear-oblancooid, the sides semiviscid, the upper ½ free;

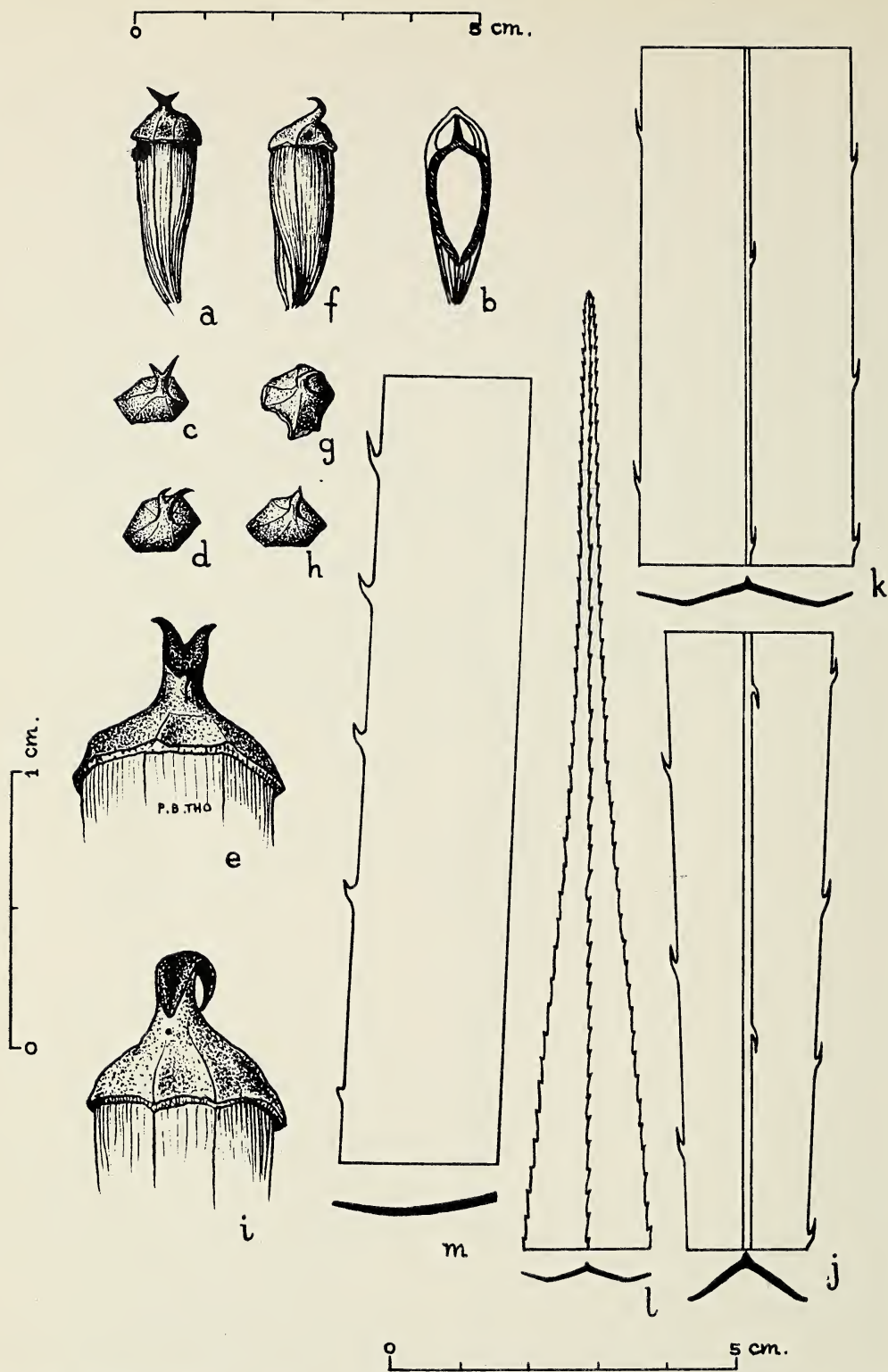


FIG. 196. *Pandanus bifidus* St. John, from holotype. *a*, Drupe, proximal view, $\times 1$; *b*, drupe, longitudinal median section, $\times 1$; *c*, *d*, lateral drupes, apical view, $\times 1$; *e*, lateral drupe and stigma, proximal view, $\times 4$; *f*, apical drupe, lateral view, $\times 1$; *g*, *h*, apical drupes, apical view, $\times 1$; *i*, apex of apical drupe and stigma, oblique view, $\times 4$; *j*, leaf base, lower side, $\times 1$; *k*, leaf middle, lower side, $\times 1$; *l*, leaf apex, lower side, $\times 1$; *m*, margins of base of mature leaf, of Kerr 20,084, $\times 1$.

endocarp inframedian, lacking distinct marginal flanges; bark grayish, unarmed; and the leaves 5 m long, 8–20 cm wide, the apex abruptly short acuminate. *P. calcis* has the syncarp 6–7 cm in diameter, subglobose, drupes 3.2–3.8 cm long, not viscid, the upper ½ free; endocarp supra-median, with large lateral flanges; bark armed with short spines; and the leaves 75–84 cm long, 2–2.7 cm wide, gradually long tapering to the subulate apex.

The new epithet is from the Latin, *calx*, lime, and is given in reference to the habitat of the species, the side cliffs or summits of precipitous limestone ridges.

SECTION *Rykia*

Pandanus bifidus sp. nov. (sect. *Rykia*)

Fig. 196

NOM. VERN.: "tôi noi."

DIAGNOSIS HOLOTYPE: Planta subcaulis, foliis 1.3 m longis 3.3 cm latis subcoriaceis gladiatis in sectione mediali cum 32 nervis secundariis parallelis in quoque latere in apice subulato breve diminuentibus et 10 cm ex apice 14 mm latis proxima basem marginibus cum aculeis 3.5–4 mm longis 25–35 mm distantibus subulatis adpressi-adscendentibus stramineis, midnervo infra cum aculeis 2.5–3 mm longis 50–58 mm distantibus simulantibus sed valde reflexis, in sectio mediali marginibus et midnervo infra cum aculeis 2.5–3 mm longis 15–48 mm distantibus adscendentibus, proxima apicem marginibus et midnervo infra cum serris 0.8–1.5 mm longis 2–7 mm distantibus, syncarpio solitario terminali 12 cm longo 10 cm diametro apparente ellipsoideo cum drupis numerosis eis 3–3.2 cm longis 8–10 mm latis 8–11 mm crassis oblongo-oblancoideis 5–7-angulosis lateribus subplanatis, parte ¼ supra libera, pileo 4–5 mm alto semiorbiculari 5–7-anguloso sublaevi tarde deciduo, stylo 3.5–5 mm longo valido osseoso corniformato eis lateralibus proximo-curvatis irregulariter bifidis vel in eis apicalibus integris et subulatis, stigmati 3–4 mm longo brunneo papilloso proximo lanceolato vel bifido, endocarpio mediali osseoso obovoideo acuminato pallido sed intra obscure brunneo lucido lateribus 1 mm crassis, seminibus 12 mm longis obovoideis, mesocarpio apicale cavernoso, meso-

carpio basali fibroso et carnosio.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Trunk from almost none to 3 m tall; leaves 1.3–3 m long, 3.3–5 cm wide, subcoriaceous, gladiate, at midsection with 32 secondary veins in each half, tapering to a short subulate apex which 10 cm down is 14 mm wide, near the base the margins with prickles 3.5–4 mm long, 20–35 mm apart, subulate, appressed ascending, stramineous; the nearby midrib below with prickles 2.5–3 mm long, 50–58 mm apart, similar but sharply reflexed; at the middle the margins and midrib below with prickles 2.5–3 mm long, 15–48 mm apart, ascending; near the apex below finely reticulate, and the margins and midrib below with serrae 0.8–2 mm long, 2–17 mm apart; syncarp solitary, terminal, 12 cm long, 10 cm in diameter, apparently ellipsoid, bearing very numerous drupes, these 3–3.2 cm long, 8–10 mm wide, 8–11 mm thick, oblong-oblancoeloid, 5–7-angled, the sides almost plane, upper ¼ free; pileus 4–5 mm high, semi-orbicular, 5–7-angled, nearly smooth, finally deciduous; style 3.5–5 mm long, stout, bony, horn-like, the lateral ones sharply curved towards apex of syncarp, irregularly bifid, or on the apical ones entire and subulate; stigma 3–4 mm long, brown, papillose, proximal, lanceolate or bifid; endocarp median, bony, obovoid, with an apical acumination, pale except for the dark brown, shiny inner surface, the lateral walls 1 mm thick; seed 12 mm long, obovoid; apical mesocarp cavernous; basal mesocarp fibrous and fleshy.

HOLOTYPE: Thailand (Siam): Pak Tong Chai, Nakawn Rachsima (=Kōrāt), marshy ground, 200 m. alt., Dec. 27, 1923, *A. F. G. Kerr* 8,132 (BK).

SPECIMENS EXAMINED: Thailand (Siam), Kao Krading, Lôi, evergreen forest, 1,200 m. alt., Feb. 11, 1931, *A. F. G. Kerr* 20,084 (BK).

DISCUSSION: *P. bifidus* St. John is a member of the section *Rykia*. Its closest relative is *P. furcatellus* Martelli from Tonkin. This has the endocarp in the lower ⅓; apical mesocarp cavernous, 10–11 mm long; and the style forks ovate, acute. In contrast *P. bifidus* has the endocarp median; apical mesocarp cavernous, 4 mm long; and the style forks subulate.

The new epithet is the Latin, *bifidus*, two-cleft, in reference to the cleft style.

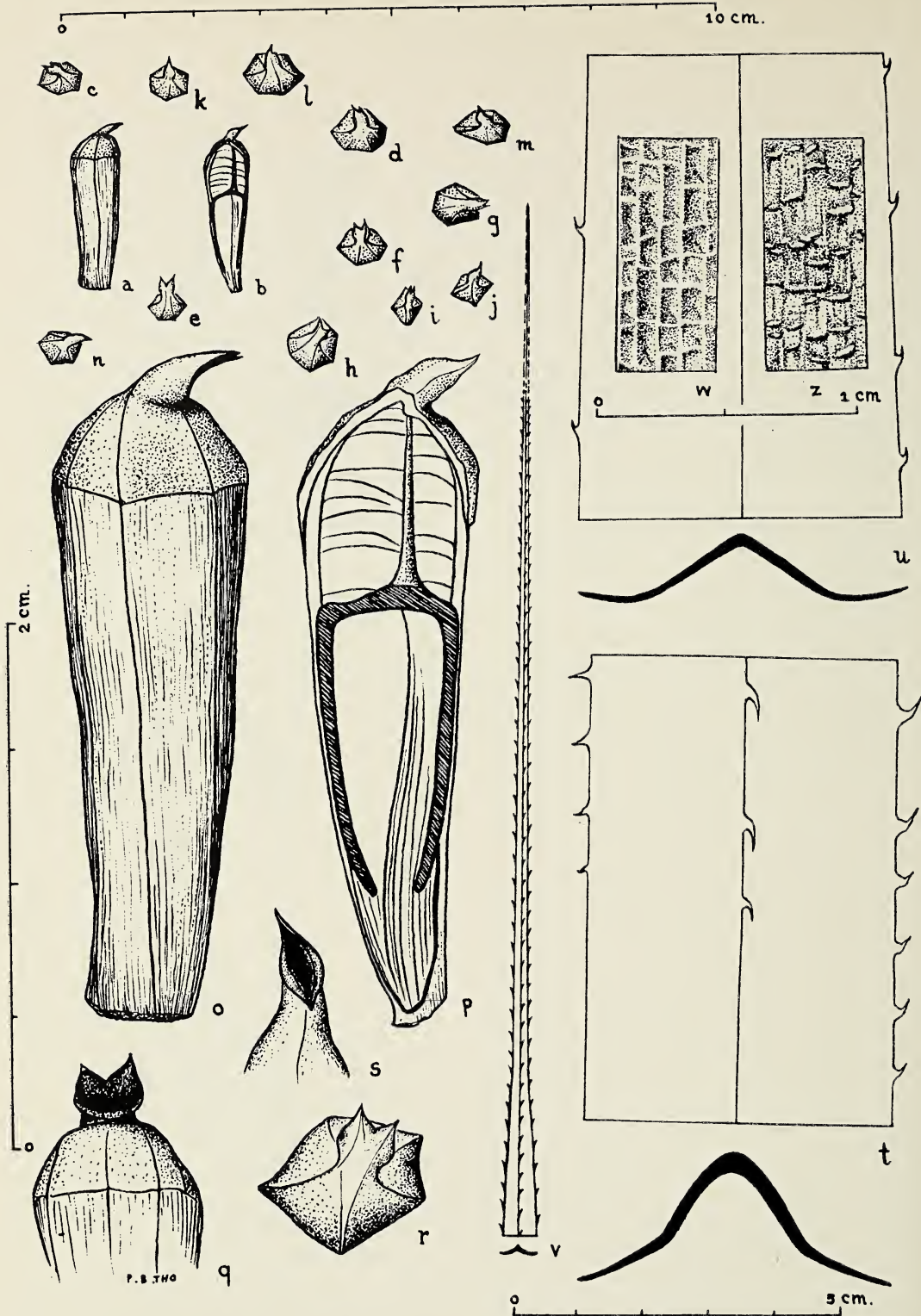


FIG. 197. *Pandanus bipollicaris* St. John, from holotype. *a*, Drupe, lateral view, $\times 1$; *b*, drupe, longitudinal median section, $\times 1$; *c-j*, lateral drupes, apical view, $\times 1$; *k-n*, apical drupes, apical view, $\times 1$; *o*, drupe, lateral view, $\times 4$; *p*, drupe, longitudinal median section, $\times 4$; *q*, apex and stigma of lateral drupe, proximal view, $\times 4$; *r*, apex of lateral drupe, apical view, $\times 4$; *s*, apex and stigma of apical drupe, proximal view, $\times 4$; *t*, leaf base, lower side, $\times 1$; *u*, leaf middle, lower side, $\times 1$; *v*, leaf apex, lower side, $\times 1$; *w*, in upper third of leaf, lower side, secondary and tertiary veins, $\times 4$; *z*, in upper third, secondary and tertiary veins, upper side, $\times 4$.

Pandanus bipollicaris sp. nov. (sect. *Rykia*)

Figs. 197, 205a, b

DIAGNOSIS HOLOTYPE: Acaulescens caespitosus 80 cm diametro, foliis 2–3 m longis 4–5 cm latis supra obscure viridibus lucidisque infra viridibus vel luteo-viridibus supra sulcatis 2-plicatis in sectione mediali cum 36 nervis secundariis parallelis in quoque latere, nervis tertiis transversis multis et in sicco conspicuis et reticulis quadratis vel oblongis formantibus, laminis ligulatis sensim per 40 cm ultimas in 10 cm apice subulato trigono contractis eo circa 10 cm ex apice 2 mm lato, basi amplexicauli inermi lucida cupracea et ex 12–15 cm marginibus cum aculeis 3–6 mm longis 10–20 mm separatis crassiter subulatis subarcuato-adscententibus stramineis vel nigris, midnervo infra ex 14–17 cm cum aculeis 4–6.5 mm longis 10–20 mm separatis crassiter subulatis arcuatis reflexis, in sectione mediali marginibus cum aculeis 2.5–3 mm longis 14–30 mm separatis arcuato-subulatis valde adscententibus basibus incrassatis, in apice contractescentibus marginibus undulatis et cum subulato-serris 1.5–2 mm longis 1.5–5 mm separatis, midnervo infra angusto et cum serris simulantibus, in apice marginibus et midnervo infra cum serrulis 0.5–0.8 mm longis 1.5–3 mm separatis, inflorescentia foeminea terminali erecta cum syncarpio solitario, pedunculo 20 cm longo 12 mm diametro trigono folioso-bracteato, syncarpio ex bracteis tandem siccis et papyraceis subclauso, syncarpio 11.5 cm longo 6.7 cm diametro ellipsoideo subtrigono viridi cum circa 672 drupis, eis 20–25 mm longis 5–9 mm latis 4–8 mm crassis anguste cuneatis apice hemisphaerico vel pyramidal-hemisphaerico 5–7-anguloso, corpore 19–22 mm longo, basi pilei 5–6 mm alto viridi glauco, stylo 3–4 mm longo brunneo lucido osseoso proxime curvato lato compresso cornuiformi bifido lobis 0.5–2 mm longis deltoideis (raro integro), stigmatibus 1.5–2.5 mm longis late ovato-lanceolatis proximis paene ad apicem productis papillois brunneis, endocarpio in parte $\frac{1}{3}$ infera oblongo-ellipsoideo apice truncato intra pallidi lucido lateribus lateralibus 0.2 mm crassis osseosis brunneis exteriori sillonati, seminibus 7–8 mm longis 3–3.5 mm diametro, mesocarpio apicali albi medullosi in media sine fibris,

mesocarpio basali 2–3 mm longo in lateribus fibroso in media carnosio.

DIAGNOSIS OF HOLOTYPE: Stemless herb with several shoots, forming a clump 80 cm in diameter; leaves 2–3 m long, 4–5 cm wide, above dark olive green and shining, below green to yellowish green, above with V-shaped furrow over the midrib and two lateral pleats, at midsection with 36 secondary parallel veins in each half, tertiary cross veins numerous and visible, but on drying conspicuous, forming squarish or oblong meshes, blade ligulate, gradually contracted in the last 40 cm to a 10 cm subulate, trigonous apex, this about 10 cm down 2 mm wide, the base amplexicaul, unarmed, shining, dull copper-colored, beginning at 12–15 cm the margins with spines 3–6 mm long, 10–20 mm apart, thick subulate, slightly upcurved, stramineous to blackish; the midrib below beginning at 14–17 cm with spines 4–6.5 mm long, 10–20 mm apart, heavy subulate, arcuate, reflexed; at midsection the margins with prickles 2.5–3 mm long, 14–30 mm apart, arcuate subulate from a thickened base, strongly ascending; the midrib below unarmed; in the contracting part near the tip the margins undulate and with subulate-serrae 1.5–2 mm long, 1.5–5 mm apart; the narrow midrib below with similar serrae; on the apex the margins and midrib below with serrulations 0.5–0.8 mm long, 1.5–3 mm apart; pistillate inflorescence terminal, erect, bearing one syncarp; peduncle 20 cm long, 12 mm in diameter, 3-sided, leafy bracted; syncarp surrounded and nearly hidden by bracts that become dry and papery; syncarp immature but apparently about full sized, 11.5 cm long, 6.7 cm in diameter, ellipsoid, slightly 3-sided, green, bearing about 672 drupes, these 20–25 mm long, 5–9 mm wide, 4–8 mm thick, narrowly cuneate, the apex hemispheric or pyramidal-hemispheric, 5–7-angled, the body 19–22 mm long; pileus with its base 5–6 mm high hemispheric or pyramidal-hemispheric, green, glaucous (immature); style 3–4 mm long, brown, shining, bony, proximally curved, broad, flattened hornlike, equally or unequally bifid, the lobes 0.5–2 mm long, deltoid (rarely unbranched this mostly on terminal drupes); stigmas 1.5–2.5 mm long, broadly ovate-lanceolate, proximal, following each lobe almost to the tip, papillose, brown; endocarp in lower $\frac{1}{3}$, oblong-ellipsoid, the apex

truncate, the inner surface pale, shining, the walls 0.2 mm thick, bony, brown, and the outer surface with sharp longitudinal ridges; seed 7–8 mm long, 3–3.5 mm in diameter; apical mesocarp of white pith, without fibers except up the sides; basal mesocarp 2–3 mm long, fibrous up the sides, fleshy within.

HOLOTYPE: Vietnam, Bach Ma, Province de Thua-Thiên, on forested stream bank, 1,400 m. alt., Jan. 26, 1961, *H. St. John* 26,379 (BISH).

DISCUSSION: *P. bipollicaris* is a member of the section *Rykia*, as is its closest relative, *P. bicornis* Ridl. of Malaya, a species which has the peduncle 5–10 cm long; syncarp 7–8 cm long, 5.6 cm in diameter, bearing 100–120 drupes, these 28–34 mm long, 8–10 mm wide; style 2–3 mm long; endocarp central, with a central apical prolongation, the lateral walls 2 mm thick; leaves 0.7–2 m long, at midsection with 24 secondary veins in each half, the blade quickly tapering into a 5 cm subulate apex, and near the base the margins with prickles 2.5–4 mm long and 2–7 mm apart. *P. bipollicaris* has the peduncle 20 cm long; syncarp 11.5 cm long, 6.7 or more cm in diameter, bearing about 672 drupes, these 20–25 mm long, 5–9 mm wide; style 3–4 mm long; endocarp in lower $\frac{1}{3}$, the apex truncate, the lateral walls 0.2 mm thick; leaves 2–3 m long, at midsection with 36 secondary veins on each side, very gradually tapering into a 10 cm subulate apex, the margins near the base with spines 3–6 mm long, 10–20 mm apart.

The epithet is the Latin adjective, *bipollicaris*, length of two thumbs or two inches, and is chosen with reference to the leaves which are about two inches wide.

Pandanus magnifibrosus sp. nov. (sect. *Rykia*)

Fig. 198

DIAGNOSIS HOLOTYPE: Planta sine caule, foliis "3.65 m. longis," 4.8 cm latis coriaceis ligulatis in sectione mediali cum 34 nervis secundariis in quoque latere in apice subulato longe diminuentibus et 10 cm ex apice solum 16 mm latis trineratis et in sectione M-formatis, in regione mediali marginibus cum aculeis 2–2.2 mm longis 8–15 mm distantibus arcuato-subulatis subluteis, midnervo infra cum aculeis 2–2.5 mm longis 9–17 mm distantibus salientibus sed api-

cibus reflexis, proxima apicem marginibus et midnervo infra cum serris 0.5–0.8 mm longis 1–4 mm distantibus et nervulis secundariis supra cum serris simulantibus 3–8 mm distantibus, "pedunculo 0.38 m. longo, syncarpio 0.34 m. ambitu," drupis numerosissimis 27–30 mm longis 3–4 mm latis et crassis anguste oblanceo-fusiformibus 5–6-angulatis, parte $\frac{3}{7}$ supera libera, pileo 12–13 mm longo arcuato lineari-lanceoloideo firmo papilloso rugosoque stramineo, stylo 5–6 mm longo subulato arcuato ad apicem vel ad basem syncarpium cartilagineo laevi et lucido, stigmate 6–7 mm longo sublineari brunneo papilloso proximo, endocarpio in parte $\frac{2}{3}$ infera et 12 mm longo pallido, seminibus non evidentis forsitan sterilibus, mesocarpio apicali et laterali conjunctis valde fibrosis et medullosis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Stemless; leaves "3.65 m. long," 4.8 cm wide, coriaceous, ligulate, at midsection with 34 secondary veins in each half, long tapering to a heavy subulate apex which 10 cm down is 16 mm wide; the base not seen; 3-nerved and in section M-shaped; at the middle the margins with prickles 2–2.2 mm long, 8–15 mm apart, arcuate-subulate, yellowish; the nearby midrib below with prickles 2–2.5 mm long, 9–17 mm apart, salient but the apex reflexed; near the apex the margins and midrib below with serrae 0.5–0.8 mm long, 1–4 mm apart, and the secondary nerves above with similar serrae 3–8 mm apart; "peduncle 0.38 m. long; syncarp 0.34 m. in circumference"; drupes very numerous, 27–30 mm long, 3–4 mm wide and thick, narrowly oblance-fusiform, 5–6-angled, the upper $\frac{3}{7}$ free; pileus 12–13 mm long, arcuate linear-lanceoloid, firm papillose and rugose, stramineous; style 5–6 mm long, subulate, curved and often recurved, cartilaginous, smooth and shining; stigma 6–7 mm long, almost linear, brown papillose, proximal; endocarp in lower $\frac{2}{3}$ and 12 mm long, pale; seeds not seen, perhaps sterile, though apparently mature; apical and lateral mesocarp continuous, strongly fibrous and pithy; basal mesocarp fibrous and fleshy.

HOLOTYPE: Thailand (Siam), Kao Soi Dao, Patalung, evergreen forest, 300 m. alt., April 29, 1930, *A. F. G. Kerr* 19,227 (BK).

DISCUSSION: *Pandanus magnifibrosus* St. John is a member of the section *Rykia*. Its closest

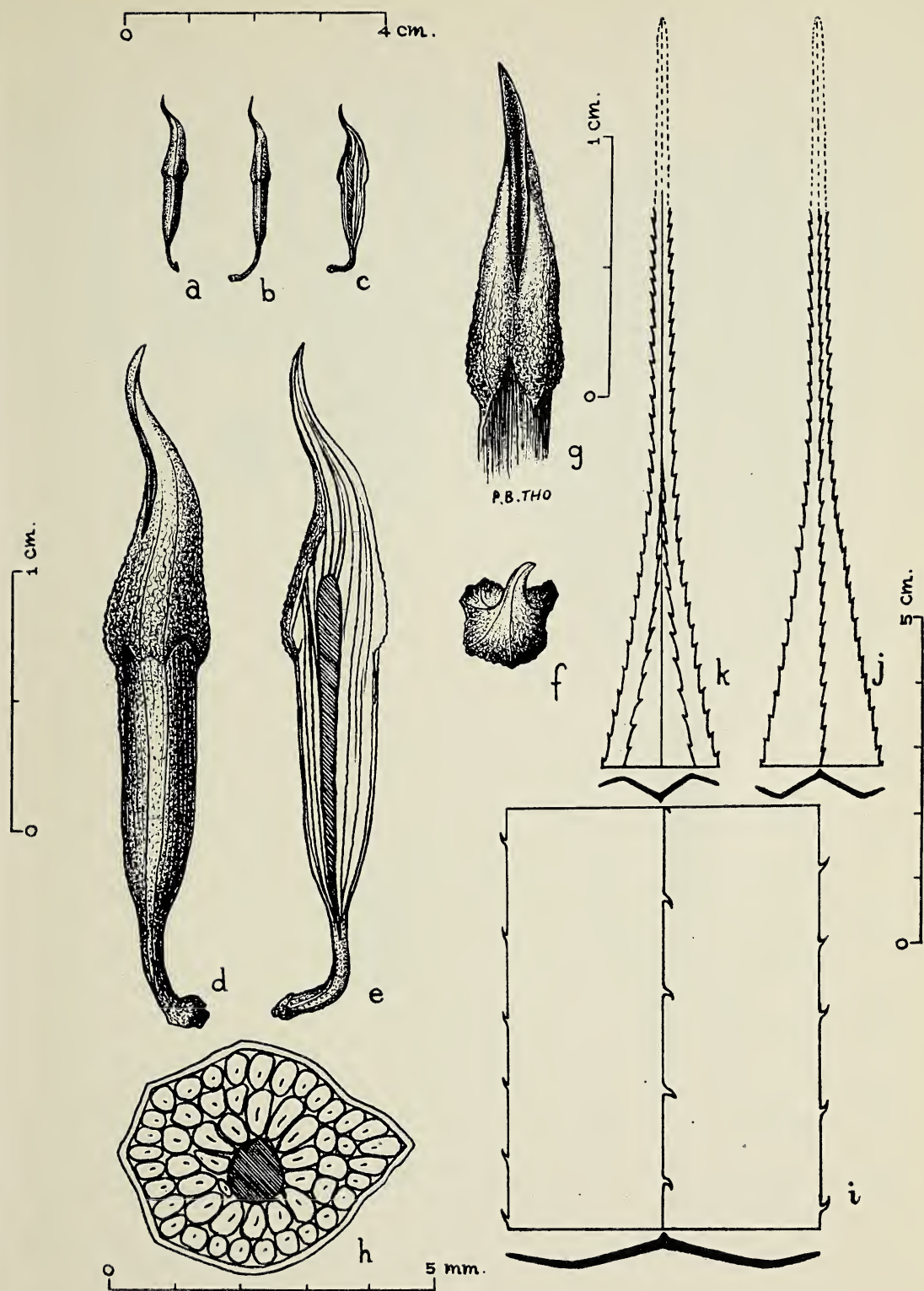


FIG. 198. *Pandanus magnifibrosus* St. John, from holotype. *a, b*, Drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, apical view, $\times 4$; *g*, drupe apex and stigma, proximal view, $\times 4$; *h*, drupe, median transverse section, $\times 10$; *i*, leaf middle, lower side, $\times 1$; *j*, leaf apex, lower side, $\times 1$; *k*, leaf apex, upper side, $\times 1$.

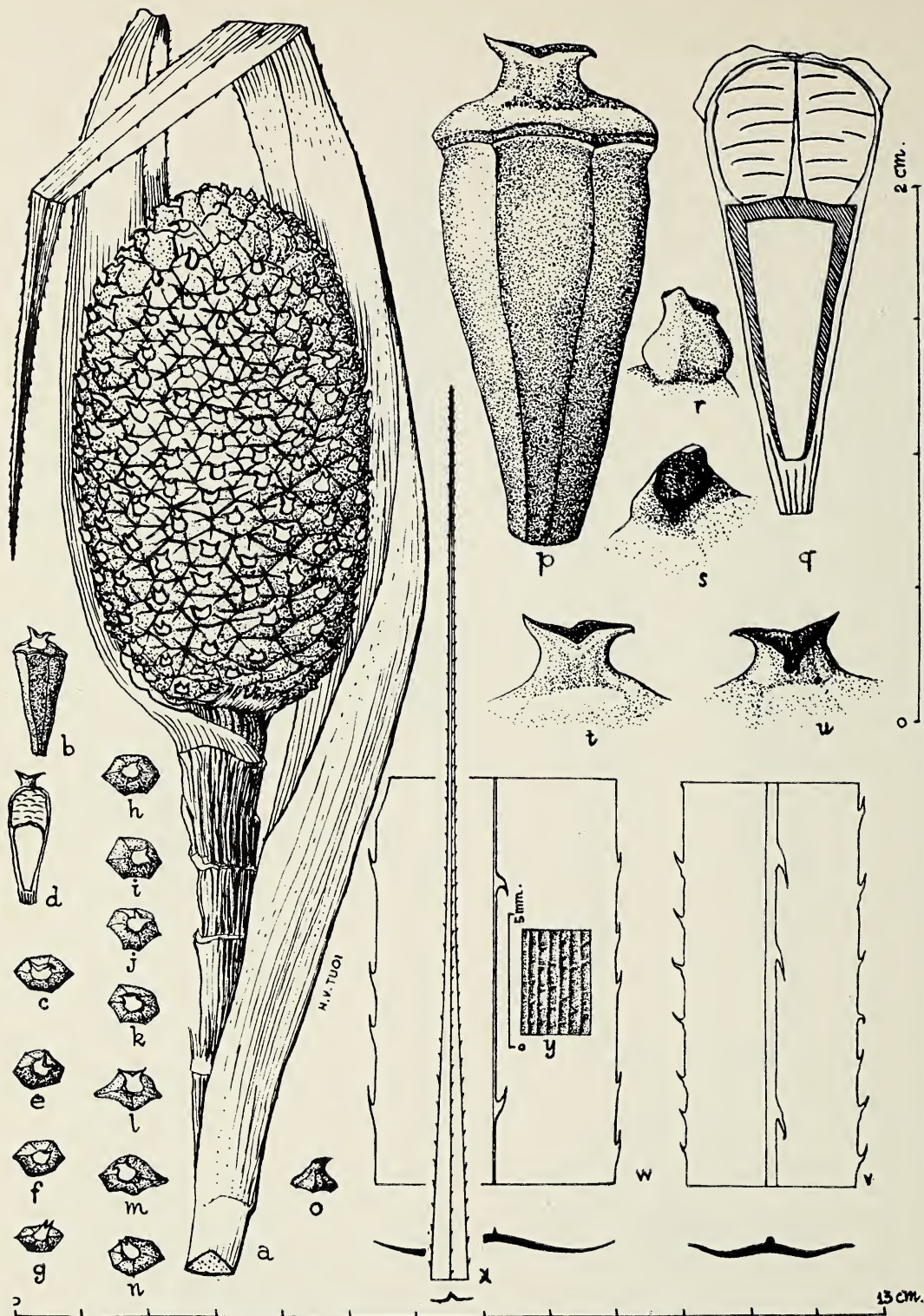


FIG. 199. *Pandanus obconicus* St. John, from the holotype. *a*, Syncarp and bracts, $\times 1$; *b*, drupe, distal view, $\times 1$; *c*, drupe, apical view, $\times 1$; *d*, drupe, longitudinal median section, $\times 1$; *e-n*, lateral drupes, apical view, $\times 1$; *o*, apical drupe, lateral view, $\times 1$; *p*, drupe, proximal view, $\times 4$; *q*, drupe, longitudinal median section, $\times 4$; *r*, apex of apical drupe and stigma, distal view, $\times 4$; *s*, stigma of apical drupe, proximal view, $\times 4$; *t*, apex of lateral drupe, distal view, $\times 4$; *u*, apex of lateral drupe and stigma, proximal view, $\times 4$; *v*, leaf base, lower side, $\times 1$; *w*, leaf middle, lower side, $\times 1$; *x*, leaf apex, lower side, $\times 1$; *y*, lower side of leaf in outer third, with secondary and tertiary veins, $\times 4$.

relative is *P. Sarasinorum* Warb. of the Celebes and Minhasa, a species having the syncarps 3.5 cm in diameter, racemose; drupes 12–14 mm long, 2 mm in diameter; style 4 mm long; and the leaf spines becoming black. In contrast, *P. magnifibrosus* has the syncarps 11.3 cm in diameter, solitary; drupes 27–30 mm long, 3–4 mm in diameter; style 5–6 mm long; and the leaf spines yellowish.

The new epithet is from the Latin, *magnus*, large, *fibrosus*, with fibers, in allusion to the very large, longitudinal fibers in the drupes.

Pandanus obconicus sp. nov. (sect. *Rykia*)

Fig. 199

DIAGNOSIS HOLOTYPI: Planta acaulescens, foliis 96 cm longis in media 3.6 cm latis proxima basem 2.7 cm latis coriaceis late sulcatis 2-plicatis in sectione mediali M-formatis et cum 37–39 nervis secundariis parallelis in quoque dimidio nervis tertiis ad basem et ad apicem conspicuis et reticulos breviter oblongos formantibus laminis gladiformatis et in apice 8–12 cm longo trigono subulato eo 10 cm ex apice 3 mm lato basi amplexicauli et inermi sed ex 5–13 cm marginibus cum aculeis 2.5–5 mm longis 7–15 mm separatis crassiter arcuatis subulatis stramineis adscendentibus, midnervo infra ex 8–15 cm cum aculeis 5–6 mm longis 12–25 mm separatis subulatis subcurvatis valde reflexis in sectione mediali marginibus cum aculeis 2–3 mm longis 6–9 mm separatis crasse subulatis adpresse adscendentibus, midnervo infra cum aculeis 3–4 mm longis remotis subulatis arcuatis basi incrassati reflexis vel adscendentibus, in apice subulato marginibus cum serris 0.5–1 mm longis 2–4 mm separatis, midnervo infra cum aculeis simulantibus 4–6 mm separatis, infructescencia terminali erecta cum syncarpio unico, pedunculo 17 cm longo 1 cm diametro trigono folioso-bracteato, bracteis superis 9–10 cm longis 4 cm latis minute serrulatis dentibus 0.2 mm longis, syncarpio 7.5 cm longo 4.5 cm diametro ellipsoideo cum circa 496 drupis eis 16–19 mm longis 7–9 mm latis 4–7 mm crassis eis terminalibus majoribus crassiter cuneiformis compressis 5–7-angulatis parte $\frac{1}{6}$ supera libera corpore 14–17 mm longo lateribus planis, pileo 3–4 mm alto basi depresso obtuso 5–7-anguloso minute papilloso, stylo 2–3 mm longo osseoso

brunneo lucido compresso proxime curvato $\frac{2}{5}$ (vel $\frac{1}{3}$ – $\frac{1}{2}$) bifido lobis plerumque divergentibus, stigmatibus 1.5–2 mm longis apicalibus vel in parte proximalibus brunneis papillosis, endocarpio infra mediali osseoso pallide brunneo lateribus 0.6–0.7 mm crassis intra obscure brunneis lucidis apice cum acumine fragili, semine 7 mm longo anguste obconico, mesocarpio apicali grandi cavernoso cum membranis medullosis albis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Plant acaulescent; leaves 96 cm long, 3.6 cm wide at the middle, 2.7 cm wide near the base, coriaceous, broadly furrowed above the midrib, 2-pleated, in section M-shaped, at midsection with 37–39 parallel secondary veins in each half, the tertiary cross veins marked near the base and the tip, forming short oblongs, and from these the outer third of the blade has a reticulate appearance, the blade sword-shaped, narrowed to an 8–12 cm trigonous subulate apex which 10 cm down is 3 mm wide, the base amplexicaul, unarmed, but beginning at 5–13 cm the margins with prickles 2.5–5 mm long, 7–15 mm apart, stout arcuate subulate, ascending, stramineous; the midrib below beginning at 8–15 cm with prickles 5–6 mm long, 12–25 mm apart, subulate, slightly curved, sharply reflexed; at the midsection the margins with prickles 2–3 mm long, 6–9 mm apart, stout subulate, appressed ascending; the midrib below with remote prickles 3–4 mm long, subulate, arcuate, with an incrassate base, reflexed or ascending as here the change-over occurs; on the subulate apex the margins with serrations 0.5–1 mm long, 2–4 mm apart; those of the midrib similar but 4–6 mm apart; infructescence terminal, erect, bearing one syncarp; peduncle 17 cm long, 1 cm in diameter, trigonous, leafy bracted, the upper bracts 9–10 cm long, 4 cm wide, minutely serrulate, the teeth 0.2 mm long; syncarp 7.5 cm long, 4.5 cm in diameter, ellipsoid, bearing about 496 drupes, these 16–19 mm long, 7–9 mm wide, 4–7 mm thick, the apical ones perceptibly the larger, thick cuneiform, compressed, 5–7-angled, upper $\frac{1}{6}$ free, the body 14–17 mm long, the sides flat; pileus 3–4 mm high, the base low obtuse, 5–7-angled, minutely papillose; style 2–3 mm long, bony, brown, shining, flattened, curved proximally, bifid usually $\frac{2}{5}$ way, rarely $\frac{1}{3}$ or $\frac{1}{2}$ way, the lobes usually divergent; stigma 1.5–2 mm long,

on the apex or partly on the proximal side of each lobe, brown, papillose; endocarp submedian, bony, pale brown, the lateral walls 0.6–0.7 mm thick, the inside surface dark brown, shiny, crowned by a weak apical acumination; seed 7 mm long, narrowly obconic; apical mesocarp a large cavern divided by white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Thailand, s. e. part, Chanturi, Makham, 100 m. alt., common along edge of savannah in scrub forest, 13 Jan. 1958, *Tem Smitinand 4,054* (SING).

DISCUSSION: *P. obconicus* is a member of the section *Rykia*, as is its closest relative, *P. horizontalis* St. John, of Vietnam, a species with peduncle 45 cm long; syncarp 10.5 cm long, 7–8 cm in diameter, with about 720 drupes, these 26–31 mm long, 9–11 mm wide; pileus base high rounded conic; endocarp in lower $\frac{1}{3}$; seed 12 mm long; stem 1.5 m tall; leaves 2.7 m long, at midsection with 33 secondary veins in each half, and near the base the midrib below with thorns 3–4 mm long, 17–35 mm apart. *P. obconicus* has the peduncle 17 cm long; syncarp 7.5 cm long, 4.5 cm in diameter, with about 496 drupes, these 16–19 mm long, 7–9 mm wide; pileus base low obtuse; endocarp submedian; seed 7 mm long; acaulescent; leaves 96 cm long, at midsection with 37–39 secondary veins in each half, and near the base the midrib below with prickles 5–6 mm long, 12–25 mm apart.

The new epithet is Latin, *ob*, inversed, *conicus*, conical, given in reference to the obconic shape of the endocarp.

Pandanus obovatus sp. nov. (sect. *Rykia*)

Fig. 200

DIAGNOSIS HOLOTYPE: Arbor "6 m. alta ramosa, trunco cum spinis parvis," foliis 1.1 m plus longis 3.1 cm latis subcoriaceis in sectione mediali cum 39 nervis secundariis in quoque dimidio gradatim ad apicem longe diminuentibus supra secundum midnervum canaliculatis marginibus reflexis, basi integra amplexicaulique sed ex 5–7 cm marginibus cum aculeis pallidis 2–2.5 mm longis 5–9 mm distantibus subulatis adscendentibus, midnervo infra per 15 cm inermi deinde cum aculeis reflexis 0.5–1 mm longis 15–18 mm distantibus subulatis, in sectione mediali marginibus cum aculeis 0.8–0.9

mm longis 7–10 mm distantibus subulatis adscendentibus, midnervo infra cum aculeis 0.3–0.5 mm longis 8–18 mm distantibus simulantibus adscendentibus, ad apicem marginibus midnervoque infra cum serrulis 0.2 mm longis 5–15 mm distantibus, syncarpio "cum 15–18 carpelibus," drupis 7.5–8.3 cm longis 4.9 cm latis 3.7 cm crassis obovoideis deltoideis laevissimis, lateribus superis laevibus brunneo-lucidis quasi ceratis et pallide multirimosus deltoideis, parte $\frac{1}{3}$ supera libera, parte $\frac{1}{2}$ infera pallide brunnea et cum dorsis et valliculis angustis longitudinalibus interobseratis, apice rotundato sed cum dorsis duobis ad stigmatem connectis, stylo corniculato compresso divergente, stigmate 8 mm longo late obovato exsulcato subverticale brunneo, endocarpio submediali parte centrali 4.3 cm longa osseosa obscure brunnea ellipsoidea muris lateralibus 2–3 mm crassis et cum humeris fortibus pallidis lateralibus submediale affixis eis oris 3.5–4.5 cm longis marginalibus crassis, semine unico 25 mm longo 9 mm diametro ellipsoideo mesocarpio laterali apicalique continuo sicco et medullosa sed cum fibris longitudinalibus, mesocarpio basali dimidio supero simulanti, dimidio infero fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree "6 m. tall, branching; stem with small spines"; leaves more than 1.1 m long, 3.1 cm wide, subcoriaceous, at midsection with 39 secondary veins in each half, gradually long tapering towards the apex, (the tip missing in ours), channeled above the midrib, the margins reflexing, the base amplexicaul and entire, but beginning 5–7 cm up the margins with pale prickles 2–2.5 mm long, 5–9 mm apart, subulate, ascending; the midrib below unarmed for 15 cm, then with reflexed prickles 0.5–1 mm long, 15–18 mm apart, subulate; at midsection the margins with prickles 0.8–0.9 mm long, 7–10 mm apart, subulate, ascending; the midrib below with similar appressed ascending prickles 0.3–0.5 mm long, 8–18 mm apart; towards the apex the margins and midrib below with serrations 0.2 mm long, 5–15 mm apart; syncarp "with 15–18 carpels"; drupes 7.5–8.3 cm long, 4.9 cm wide, 3.7 cm thick, obovoid, 3-sided, very light, the upper sides smooth, brown and shiny as if varnished and with many pale longitudinal cracks, 3-angled, upper $\frac{1}{3}$ free, lower half pale brown and with several sharp longitudinal ridges and

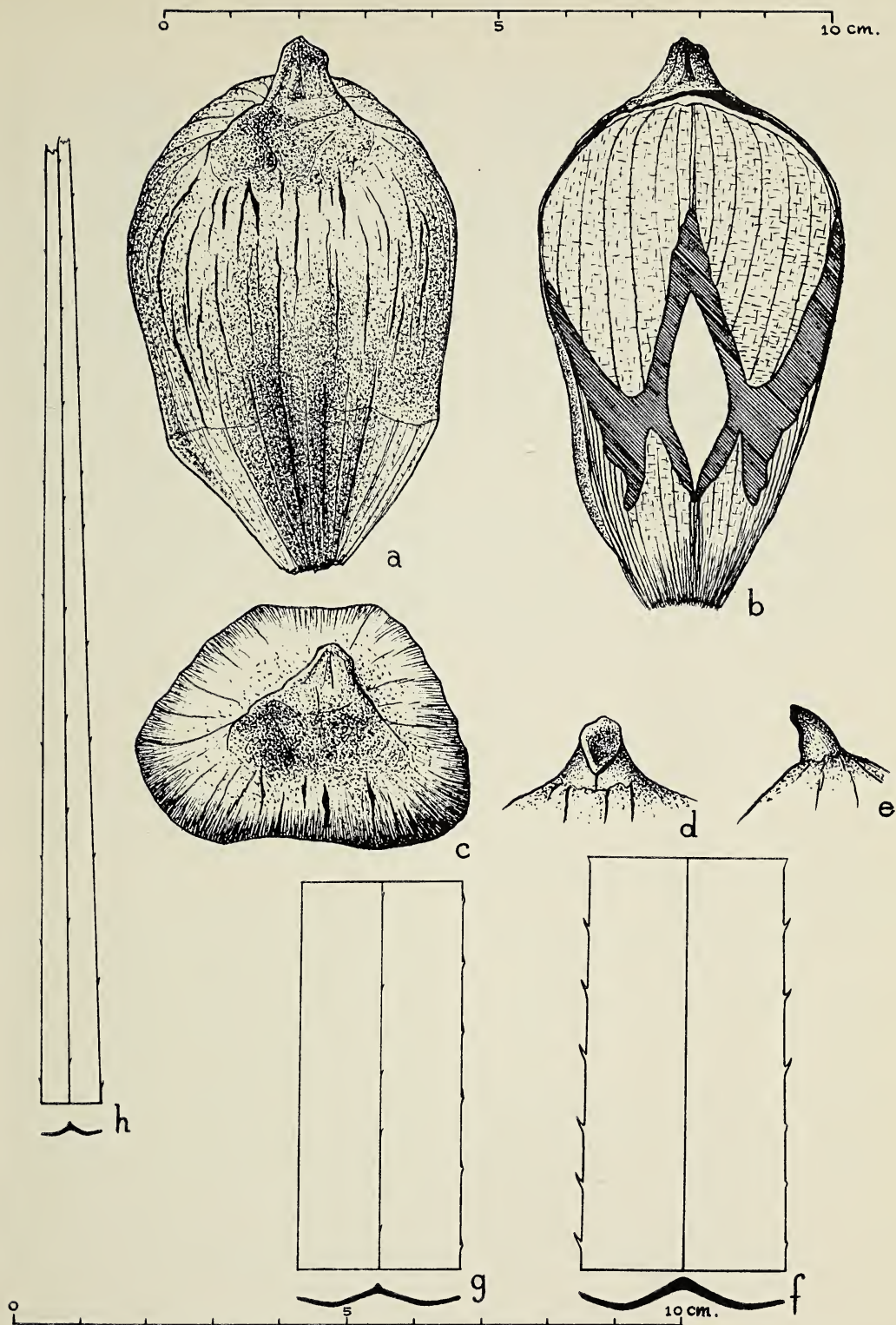


FIG. 200. *Pandanus obovatus* St. John, from holotype. *a*, Drupe, lateral view, $\times 1$; *b*, drupe, longitudinal median section, $\times 1$; *c*, drupe, apical view, $\times 1$; *d*, stigma, proximal view, $\times 1$; *e*, apex of drupe, lateral view, $\times 1$; *f*, leaf base, lower side, $\times 1$; *g*, leaf middle, lower side, $\times 1$; *h*, leaf apex, lower side, $\times 1$.

valleys like mortising angles, the apex rounded but from each of two angles a ridge mounts to support the stigma on a flattened, overhanging process or style; stigma 8 mm long, broadly obovate, without crease, nearly vertical, brown; endocarp submedian, the central part 4.3 cm long, bony, dark brown, and ellipsoid, its lateral walls 2–3 mm thick, a little below the middle of this central endocarp are heavy, pale, lateral shoulders bearing heavy marginal flanges 3.5–4.5 cm long; seed solitary, 25 mm long, 9 mm in diameter, ellipsoid; lateral and apical mesocarp continuous, dry and pithy but with longitudinal fibers, and this pithy mesocarp also occupies the upper half of the area below the endocarp, the remaining basal area fibrous and fleshy.

HOLOTYPE: Thailand (Siam): Mënam Pasak, Keng Koi, on rocky limestone hill, Dec. 9, 1923, A. F. G. Kerr 7,669 (BK).

DISCUSSION: *P. obovatus* is a member of the section *Rykia*, though with its large, dry, pithy drupes it is unique and without a close relative. It can be compared to *P. borneensis* Warb. which has the syncarp spicate, 6–8 cm long; drupe apex 10–12 mm broad; and the style 2 mm long. In *P. obovatus* the syncarp is solitary, about 23 cm long; drupe apex 4.9 cm broad; and the style 11 mm long, horn-like, flattened.

The type specimen consists of a leaf minus the tip, and three fruit halves, yet so unique is the species that this much suffices. There are no really close relatives known.

The new epithet is the Latin *obovatus*, referring to the obovate profile of the drupes.

Pandanus reticulosus sp. nov. (sect. *Rykia*)

Fig. 201

NOM. VERN.: "toei yai" (= *Pandanus big*).

DIAGNOSIS HOLOTYPE: Licet acaulescens, foliis 2 m longis 5 cm latis in medio 3.8 cm latis circa basem coriaceis reticulatis in sectione mediale cum 33 nervis secundariis parallelis fortibus in quoque dimidio, nervis tertiis transversis fortibus elevatis et reticulam quadratorum vel oblongorum brevium formantibus, laminis ligulatis sed subabrupte in apice circa 10 cm longo caudato trigono subulato diminuentibus eo circa 10 cm ex apice 5 mm lato, basi amplexicauli et inermi pallida sed ex 7–15 cm marginibus cum aculeis

3–5 mm longis 12–22 mm separatis subulatis curvatis fortibus pallidis adscendentibus, midnervo infra ex 12.5 cm cum aculeis 3–6 mm longis 32–65 mm separatis arcuato-subulatis reflexis, in sectione mediali marginibus cum aculeis 2.8–3 mm longis 14–24 mm separatis arcuatis subulatis adscendentibus, midnervo infra inermi, in apice subulato marginibus cum serrulis 0.6–1 mm longis 1–3 mm separatis, midnervo infra cum serrulis 0.3–0.8 mm longis 3–4 mm separatis, pedunculo "brevi," syncarpio solitario 7 cm longo 5.5 cm diametro latiter ellipsoideo purpurascenti cum 113 drupis, eis 22–26 mm longis 9–14 mm latis 9–11 mm crassis ob lanceoloideis basi truncata 6-angulosis parte ¼ supera libera, corpore 18–22 mm longo lateribus planis, pileo 6–8 mm alto basi 4–5 mm alto semiorbiculari vel depresso semiorbiculari rugosa exlaevi minime 6-angulosa, stylo 2.5–5 mm longo osseoso brunneo lucido compresso proxime curvato eis druparum lateralium plerumque breviter bifidis sed aliquis basalibus subulatis, stigmatibus 1–1.5 mm longo cordato vel late cordato brunneo papilloso in apice proximali cavernoso affixi, endocarpio mediali 11 mm longo osseoso extus pallidi lateribus 0.8 mm crassis intra obscure brunneis et lucidis, seminibus 10 mm longis 8 mm diametro obovoideis, mesocarpio apicali aerenchymati cum membranis latis transversis albis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Apparently acaulescent, gregarious on ground among undershrubs; leaves 2 m long, 5 cm wide at the middle, 3.8 cm wide near the base, coriaceous, reticulately veined and conspicuously so in outer half, at midsection with 33 parallel secondary veins in each half, the tertiary cross veins heavy, raised, forming a reticulum of squares or short oblongs, blade ligulate, rather abruptly narrowed to a caudate trigonous subulate apex about 10 cm long, this about 10 cm down 5 mm wide, the base amplexicaul and unarmed, pale, but beginning 7–15 cm up the margins with spines 3–5 mm long, 12–22 mm apart, stout curved subulate, ascending, pale; the midrib below beginning at 12.5 cm with spines 3–6 mm long, 32–65 mm apart, arcuate subulate, reflexed; at midsection the margins with prickles 2.8–3 mm long, 14–24 mm apart, arcuate subulate, ascend-

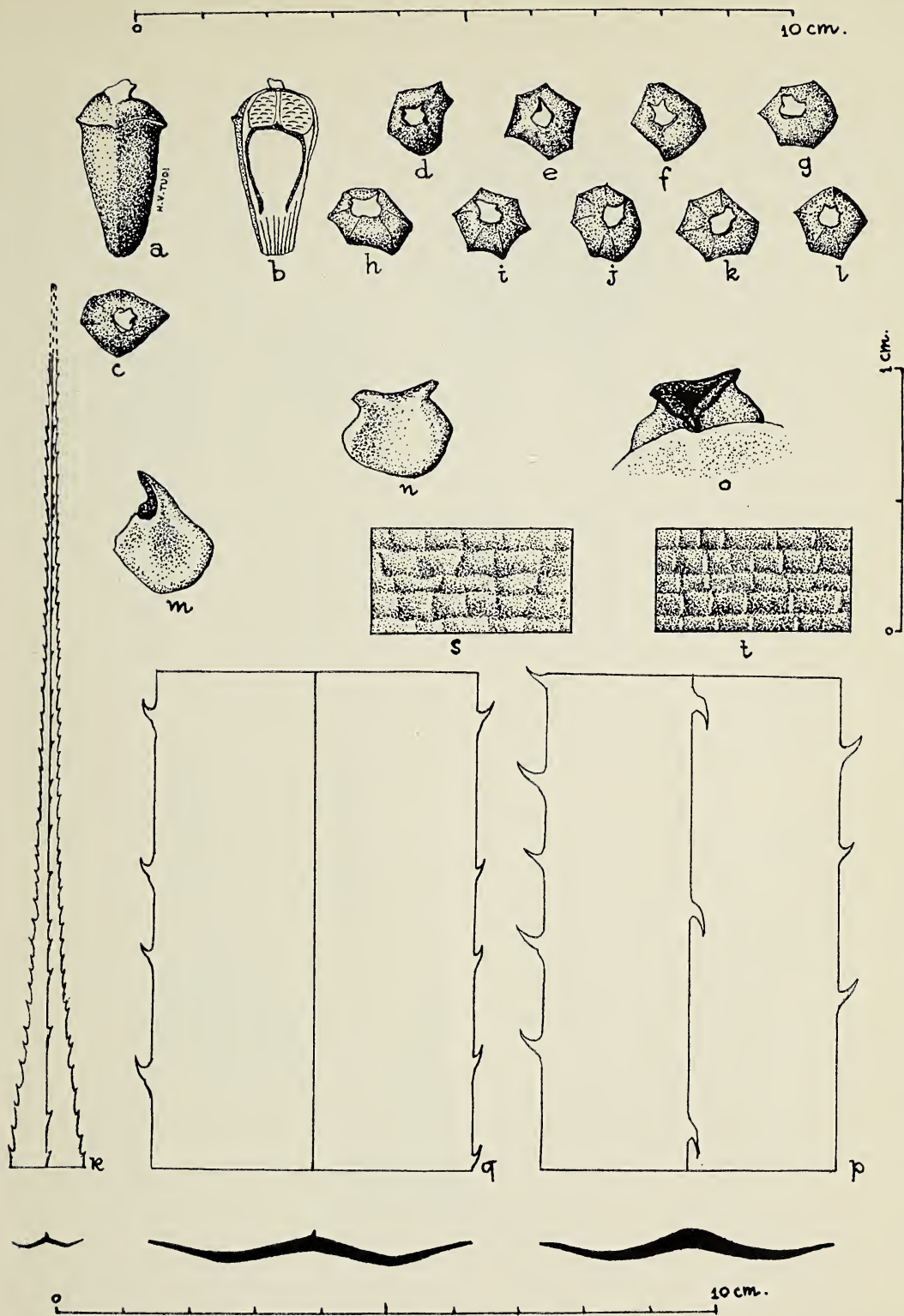


FIG. 201. *Pandanus reticulosus* St. John, from holotype. *a*, Drupe, lateral view, $\times 1$; *b*, drupe, longitudinal median section, $\times 1$; *c-l*, drupe, apical view, $\times 1$; (*d* and *f* are the most common kinds; *e* is basal, rarely lateral); *m*, apex of apical drupe and stigma, lateral view, $\times 4$; *n*, apex of lateral drupe, oblique view, $\times 4$; *o*, apex of lateral drupe and stigma, proximal view, $\times 4$; *p*, leaf base, lower side, $\times 1$; *q*, leaf middle, lower side, $\times 1$; *r*, leaf apex, lower side, $\times 1$; *s*, leaf middle, upper side, secondary and tertiary veins, $\times 4$; *t*, leaf middle, lower side, secondary and tertiary veins, $\times 4$.

ing; the midrib below unarmed; on the subulate apex the margins with serrations 0.6–1 mm long, 1–3 mm apart; the midrib below with serrations 0.3–0.8 mm long, 3–4 mm apart; peduncle "short"; syncarp single, 7 cm long, 5.5 cm in diameter, broadly ellipsoid, purplish, bearing 113 drupes, these 22–26 mm long, 9–14 mm wide, 9–11 mm thick, oblanceoloid from a truncate base, 6-angled, upper $\frac{1}{4}$ free, the body 18–22 mm long, with flat sides; pileus 6–8 mm high, its base 4–5 mm high, semiorbicular or oblately so, the surface roughened, dull, weakly 6-angled; style 2.5–5 mm long, bony, brown, shining, flattened, proximally curved, the lateral ones mostly shortly bifid, but some of the basal ones with a single, subulate tip; stigma 1–1.5 mm long, cordate or broadly so, brown, papillose, in the hollow proximal tip; endocarp median, 11 mm long, bony, pale without, the walls 0.8 mm thick, within dark brown and shining; seed 10 mm long, 8 mm in diameter, obovoid; apical mesocarp an aerenchyma with broad transverse, white membranes; basal mesocarp fibrous and fleshy.

HOLOTYPE: Thailand, n. e. region, Loei, Phu Krading, Tham Saw, common in evergreen forest, 1,300 m. alt., *Tem Smitinand* 406 (BKF no. 11,999).

DISCUSSION: *P. reticulosus* is a member of the section *Rykia*, as is its closest relative, *P. bicornis* Ridl. of Malaya, a species which has the syncarp 15 cm long; drupes 34 mm long; style forks spreading and with the tips recurved; seed 6 mm long, cylindric; and the leaf margin near the base with spines 2.5–4 mm long, and 2–7 mm apart. *P. reticulosus* has the syncarp 7 cm long; drupes 22–26 mm long; style forks ascending or diverging; seed 10 mm long, obovoid; and the leaf margin near the base with spines 3–5 mm long, and 12–22 mm apart.

The new epithet is the Latin adjective, *reticulosus*, with a network, and is given in reference to the reticulate venation of the leaves.

Pandanus thailandicus sp. nov. (sect. *Rykia*)

Figs. 202, 203

NOM. VERN.: "toei nām."

DIAGNOSIS HOLOTYPE: Frutex 1.5 m altus ramosus, foliis 35–37 cm longis 6–8 mm latis subcoriaceis ligulatis planatis vel marginibus

paene involutis in sectione mediali cum 13 nervis secundariis parallelis in quoque dimidio parte $\frac{1}{3}$ supera sensim in apice subulato diminuenti 10 cm ex apice 4 mm lata in sicco pallidis et infra subglaucis in basi amplexicaulibus et integris proxima basem marginibus cum aculeis 1.8–2.2 mm longis 8–15 mm separatis adscendentibus arcuato-subulatis stramineis, midnervo infra cum aculeis 2.2–2.5 mm longis 8–25 mm distantibus simulantibus adscendentibus, in sectione mediali marginibus cum aculeis 1.3–1.8 mm longis 4–7 mm separatis simulantibus sed subadpressis, midnervo infra cum aculeis 1.7–2 mm longis 6–15 mm separatis simulantibus adscendentibus, proxima apicem marginibus cum serris 0.1–0.3 mm longis 1–4 mm separatis adpressis cum apicibus subulatis, midnervo infra cum serris 0.2–0.6 mm longis 2.5–6 mm separatis simulantibus, pedunculo terminali 7 cm longo 3–4 mm diametro folioso-bracteato, syncarpio solitario pendenti 36 mm longo, 35 mm diametro elliptico-subgloboso cum circa 230 drupis, eis 14–16 mm longis 4–4.2 mm latis 3 mm crassis anguste oblanceoloideis 5–7-angulis lateribus subcurvatis parte $\frac{1}{4}$ supera libera, pileo conico sed in sicco cum rugis longitudinalibus, stylo 2.5–3 mm longo crasse subulato cartilagineo pallido proximo-curvato, stigmate 2–2.5 mm longo lanceolato proximo brunneo papilloso, endocarpio centrali 6 mm longo anguste obovoideo cartilagineo obscure brunneo intra lucido lateribus 0.1 mm crassis, mesocarpio apicali lateralique conjuncto sicco et meduloso, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Branching shrub 1.5 m tall; stem 8–10 mm in diameter, yellowish, unarmed; prop roots not mentioned; leaves 35–50 cm long, 6–10 mm wide, subcoriaceous, ligulate, flat or the margins slightly involute, at midsection with 13 parallel secondary veins in each half, the upper $\frac{1}{3}$ gradually tapering to the acute tip, this 10 cm from the apex 4 mm wide, when dried pale and below somewhat glaucous, the very base amplexicaul and unarmed, near the base the margins with prickles 1.8–2.2 mm long, 8–15 mm apart, ascending, arcuate subulate, stramineous; the nearby midrib below with similar ascending prickles 2.2–2.5 mm long, 8–25 mm apart; at midsection the margins with prickles 1.3–1.8 mm long, 4–7 mm apart, similar but subap-

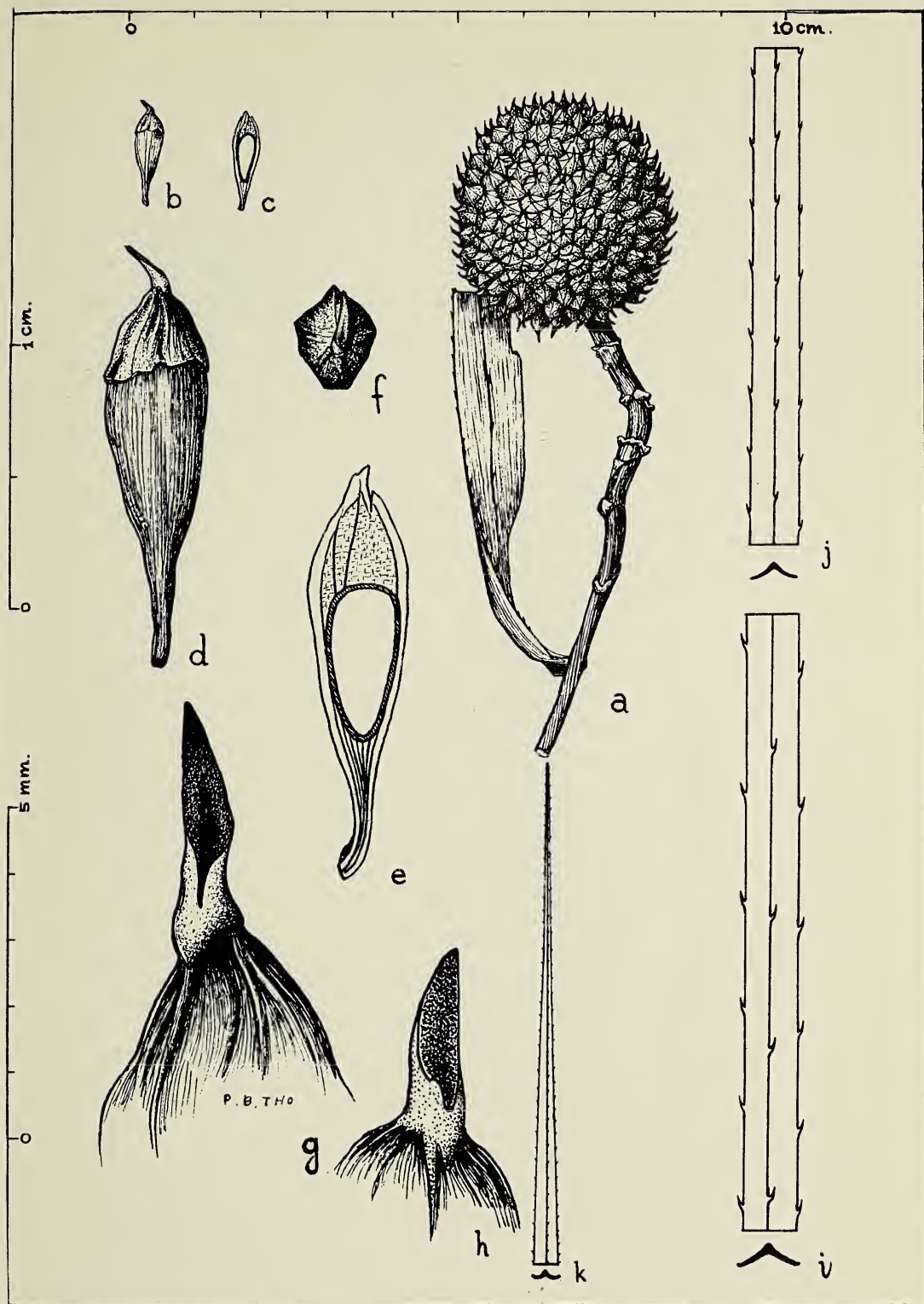


FIG. 202. *Pandanus thailandicus* St. John, from holotype. *a*, Syncarp, $\times 1$; *b*, drupe, lateral view, $\times 1$; *c*, drupe, longitudinal median section, $\times 1$; *d*, drupe, lateral view, $\times 4$; *e*, drupe, longitudinal median section, $\times 4$; *f*, drupe, apical view, $\times 4$; *g*, *h*, apex of drupe and stigma, proximal view, $\times 10$; *i*, leaf base, lower side, $\times 1$; *j*, leaf middle, lower side, $\times 1$; *k*, leaf apex, lower side, $\times 1$.

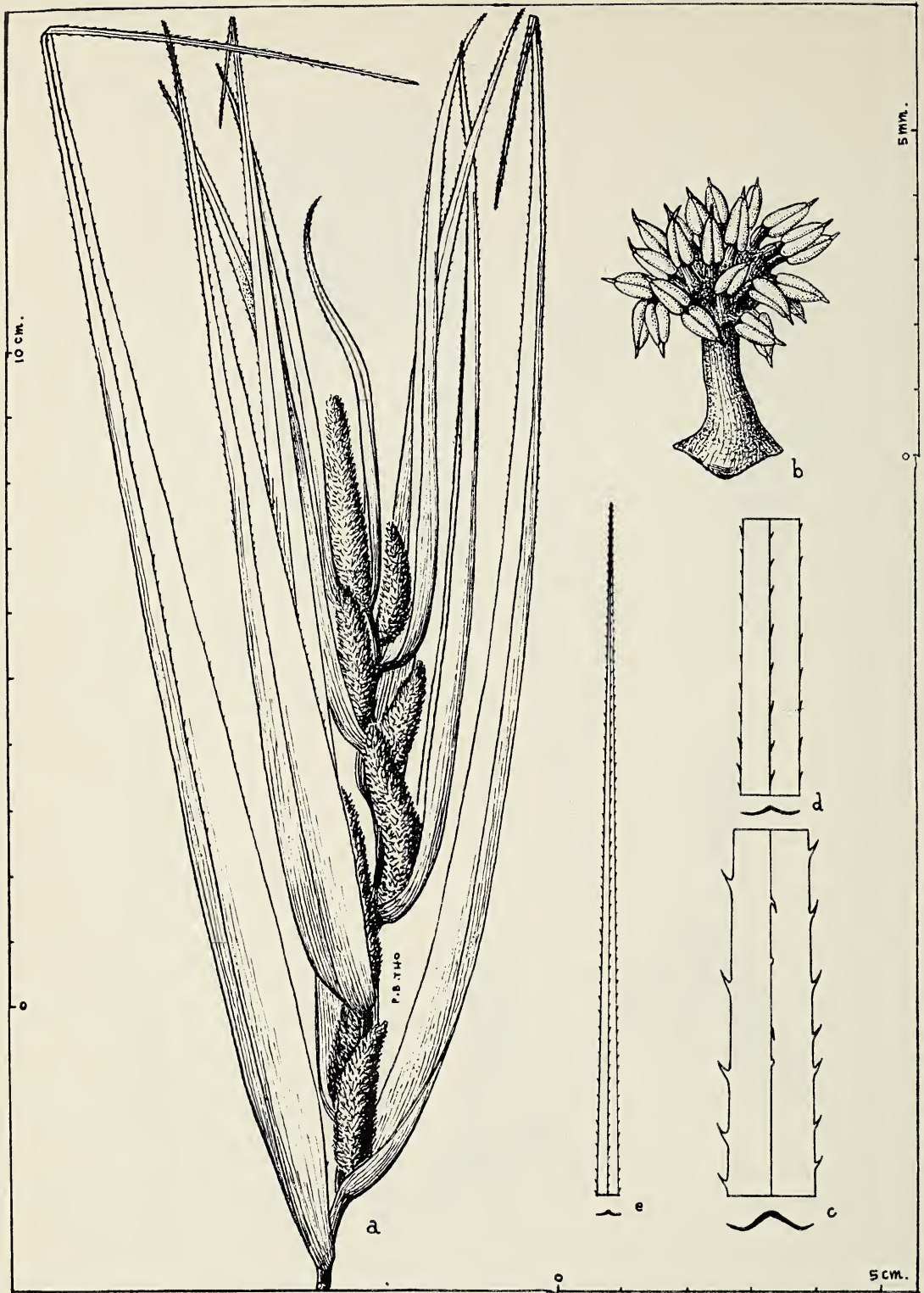


FIG. 203. *Pandanus thailandicus* St. John, from *Dee Bun Phong* 914. *a*, Staminate inflorescence, $\times 1$; *b*, column and anthers, $\times 10$; *c*, leaf base, lower side, $\times 1$; *d*, leaf middle, lower side, $\times 1$; *e*, leaf apex, lower side, $\times 1$.

pressed; the midrib below with similar prickles 1.7–2 mm long, 6–15 mm apart, ascending; near the apex the margins with subulate-tipped appressed serrations 0.1–0.3 mm long, 1–4 mm apart; those of the midrib below similar but 0.2–0.6 mm long, 2.5–6 mm apart; peduncle terminal, 7–12 cm long, 3–4 mm in diameter, with many leafy bracts, the median ones 21 cm long, 8 mm wide, the upper ones 7 cm long, 17 mm wide, foliaceous, white; syncarp single, pendent, elliptic-subglobose, 36–55 mm long, 35–42 mm in diameter, bearing 230–592 drupes, these 14–19 mm long, 4–4.2 mm wide, 3 mm thick, narrowly oblanceoloid, 5–7-angled, the sides gently curving, upper $\frac{1}{4}$ free; pileus conic, but when dry with longitudinal wrinkles, the base connate with adjacent ones, leaving no visible suture; style 2–3.5 mm long, stout subulate, pale, cartilaginous, curved upward towards apex of syncarp (or the basal ones curved distally); stigma 1.5–2.5 mm long, lanceolate, proximal, brown papillose; endocarp central, 6 mm long, narrowly obovoid, cartilaginous, brown, shiny within, the walls 0.1 mm thick; apical and lateral mesocarps continuous, dry pithy; basal mesocarp fibrous and fleshy.

STAMINATE PLANT: Stem 8 cm or a little more in height, 7–10 mm in diameter, dark brown, striate, shining; leaves numerous in terminal tuft, 46–48 cm long, just above the base 12–13 mm wide, at the middle 7–8 mm wide, green, secondary parallel veins prominent throughout and at midsection 14 in each half, the base amplexicaul, unarmed, softer, beginning 3.5–4 cm up the margins with prickles 2.3–3.5 mm long, 5–15 mm apart, arcuate, heavy subulate, ascending, yellow; the nearby midrib below beginning at 5–5.5 cm with prickles 2–2.5 mm long, 6–15 mm apart, similar but reflexed, at the point of reversal of direction often paired; at midsection the margin and midrib below with similar prickles 1–2.5 mm long, 4–6 mm apart, ascending; staminate inflorescence terminal; peduncle 6 cm long, 1.5 mm in diameter, leafy bracted; floral part 11 cm long; lowest floral bract about 45 cm long, the base 15 mm wide, soft, white, veiny, unarmed, narrowly lanceolate, the upper part 6 mm wide, green, subcoriaceous, at midsection the margins with prickles 0.5–1 mm long, 2–3 mm apart, arcuate subulate, ascending, yellow; the midrib below with similar

ones 0.3–0.5 mm long, 1.5–3 mm apart; the 7 spikes fragrant, 2.3–3 cm long, 6–8 mm in diameter, narrowly ellipsoid, densely flowered; stamens numerous, in fascicles; staminal column 2–2.5 mm long, stout, but tapering upwards; free filament tips 0.5 mm long; anthers 0.7–0.8 mm long, lanceolate, bearing on its apex a subulate projection of the connective 0.2 mm long.

HOLOTYPE: Thailand (Siam): Pü Wieng, Kawn Ken, by dry stream bed, 300 m. alt., Feb. 7, 1931, *A. F. G. Kerr* 20,016 (BK).

SPECIMENS EXAMINED: Thailand (Siam), Bung, Ubon, by stream in open forest, 100 m. alt., Jan. 29, 1924, *A. F. G. Kerr* 8,365 (BK); n. e. part, Loei, Phu Luang, by stream, 1,000 m. alt., 24 Sept. 1957, *Dee Bun Pheng* 914, staminate and pistillate (BKF no. 16,154).

DISCUSSION: *P. thailandicus* is a member of the section *Rykia*, as is its closest relative, *P. immersus* Ridl. of Malaya, a species with the syncarp (immature) 9.5 cm long, 6 cm in diameter, ellipsoid, with about 1,440 drupes, these 5–6 mm wide; pileus 7–8 mm long; style 4–6 mm long; plant aquatic; leaves "many feet long," 10.2 cm wide, caudate subulate apex 30 cm long, at midsection with 70 secondary veins in each half, and the margins with prickles 2.5–4 mm long, 9–18 mm apart. *P. thailandicus* has the syncarp 3.6–5.5 cm long, 3.5–4.2 cm in diameter, elliptic-subglobose, with 230–592 drupes, these 4–4.2 mm wide; pileus 3.5–6 mm long; style 2–3.5 mm long; plant terrestrial; leaves 35–50 cm long, 6–10 mm wide, the subulate apex 7 cm long, at midsection with 13 veins in each half and the margins with prickles 1.3–1.8 mm long and 4–7 mm apart.

The new epithet is geographic, referring to the native country of the species.

Pandanus unicornutus sp. nov. (sect. *Rykia*)

Fig. 204

NOM. VERN.: "chawng lī"; "tôi yai."

DIAGNOSIS HOLOTYPI: Arbor ad 8 m alta ramosa, foliis "ad 3.5 m. longis" 10–11 cm latis proxima basem crassiter coriaceis in apice subulato 8 cm longo abrupte contractis eo 10 cm ex apice 7 mm lato in sectio late M-formatis in puncto 30 cm ex basi cum 70 nervis secundariis in quoque latere, basi integra et amplexicauli sed ex 15 cm marginibus cum spinis 4.5–6 mm longis



FIG. 205a. *Pandanus bipollicaris* St. John, from holotype. Branch, leaves, and syncarp.

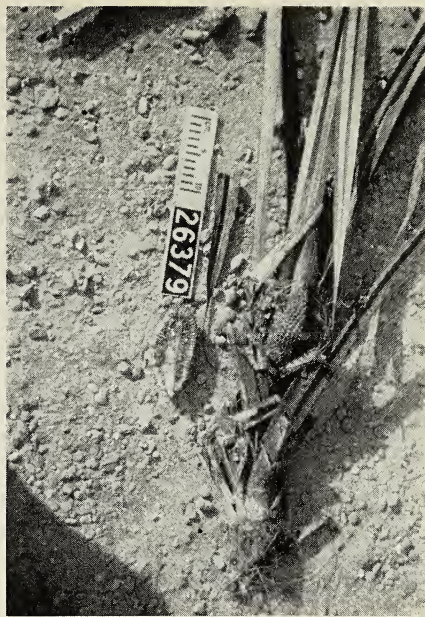


FIG. 205b. *Pandanus bipollicaris* St. John, from holotype. Branch, leaves, and syncarp, and longitudinal median section of syncarp.

7–15 mm distantibus basi crassa apice subulato subarcuatis divergentibus vel subadscendentibus pallide brunneis, midnervo infra cum spinis 4–5 mm longis 10–41 mm distantibus crasse conico-subulatis reflexis, in sectio mediali foliis 12.5–13 cm latis in paginis ambis rugoso-reticulatis marginibus cum spinis 4–6 mm longis 21–38 mm distantibus adscendentibus basi crassa apice crassiter subulato, midnervo inermi, proxima apicem marginibus et midnervo infra cum serris subulatis 0.5–0.8 mm longis 2–4 mm distantibus paginis ambis rugoso-reticulatis, laminis in sectio M-formatis fere ad apicem, spicis cum 7 syncarpiis, "syncarpio maximo 15 cm. longo" 11 cm diametro, drupis multis 3.5–3.9 cm longis 8–10 mm latis crassisque anguste ellipsoideis lateribus laevibus planis vel subcurvatis 5-angulatis parte 1/7 supera libera, pileo oblato-semiorbiculari firmo quoque solum dehiscenti, stylo 6–8 mm longo osseoso corniformi integri (rariter bifido) proxime curvato pallide brunneo, stigmatibus 3–4 mm longo lanceolato brunneo papilloso, endocarpio submediali 25 mm longo lateribus 0.1 mm crassis cartilagineo stramineo pagina interiori lucido apice lanceoloideo producto, seminibus 15–16 mm longis 5–6 mm

diametro ellipsoideo, mesocarpio apicali in marginibus fibroso intra cavernoso, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 7–15 m tall, 17–20 cm in diameter, branching; bark pale, with short spines; "prop roots to 1 m. long, 5–8 cm. in diameter, armed with short spines"; leaves "3.2–3.85 m. long," 8.4–11 cm wide near the base, thick coriaceous, abruptly acuminate to a subulate apex 8 cm long, the tip 10 cm down from the apex 7 mm wide, very wide M-shaped in section, at 30 cm from the base with 70 secondary veins in each half, the base entire and amplexicaul, but beginning 15 cm up the margins with thorns 4.5–7 mm long, 7–15 mm apart, heavy based, subulate-tipped, somewhat arcuate, divergent or slightly ascending, pale brownish; the midrib below with thorns 4–5 mm long, 10–14 mm apart, heavy conic-subulate, reflexed; at midsection 12.5–13 cm wide, both surfaces rugose reticulate, the margins with thorns 4–6 mm long, 21–38 mm apart, ascending, the base heavy, the tip thick subulate; the nearby midrib prominent but unarmed; near the apex the margins and midrib below subulate-serrate, the teeth 0.5–0.8 mm

long, 2–4 mm apart, both the upper and lower surfaces rugose-reticulate from the heavy cross veinlets, the blade M-shaped in section and the pleats running almost to the tip; peduncle 70 cm long; spike with 5–7 syncarps, the largest 14–18 cm long, 11–12 cm in diameter, ovoid but distinctly 3-sided; drupes numerous, these 3.5–4.3 cm long, 8–10 mm wide and thick, narrowly ellipsoid, the sides smooth, plane or gently curved, 5-angled, upper $1/7$ free; pileus oblate-semiorbicular, firm, shedding singly, ending in a style 6–8 mm long, bony, horn-like, entire (rarely bifid), strongly curved towards the apex of the syncarp, pale brownish; stigma 3–4 mm long, lanceolate, brown papillose; endocarp slightly submedian, 25 mm long, the lateral walls 0.1 mm thick, cartilaginous, stramineous, the inner surface shining, the apex produced upwards into a long lanceoloid tip; seeds 15–16 mm long, 5–6 mm in diameter, ellipsoid; apical mesocarp fibrous around the margin, cavernous within; basal mesocarp fibrous and fleshy.

HOLOTYPE: Thailand (Siam), Kaw Tao, Surat, in high evergreen forest, under 5 m. alt., April 16, 1927, *A. F. G. Kerr* 12,772 (BK).

SPECIMENS EXAMINED: Thailand (Siam), Kaw Tao, Surat, evergreen forest, 300 m. alt., Sept. 21, 1928, *A. F. G. Kerr* 16,052 (BK); Wangka, Kanburi, by stream in evergreen forest, 700 m. alt., Feb. 3, 1926, *A. F. G. Kerr* 10,432 (BK); Ta Ngaw, Chumpawn, common along streams in savannah evergreen [forest], Jan. 22, 1927, *A. F. G. Kerr* 11,601 (BK).

DISCUSSION: *Pandanus unicornatus* is a member of the section *Rykia*, as is its closest relative, *P. penangensis* Ridley, a Malayan species which has the drupes 42–47 mm long, 6–7 mm thick; endocarp 32–33 mm long, the lateral walls 1–1.5 mm thick; and the leaves 12 cm wide, near the base the margins with prickles 1.3–1.5 mm long, 4–7 mm apart. *P. unicornatus* has the drupes 35–43 mm long, 8–10 mm thick; endocarp 25 mm long, the lateral walls 0.1 mm thick; and the leaves 10–11 cm wide, near the base the margins with spines 4.5–6 mm long, 7–15 mm apart.

The epithet is from the Latin *unus*, one, *cornutus*, with a horn, in allusion to the usual single hornlike style.

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